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Survival and Development of Lake Trout (*Salvelinus namaycush*) embryos in an Acidified Lake in Northwestern Ontario

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Mohr, L. C., K. H. Mills, and J. F. Klaverkamp. 1990. Survival and development of lake trout (*Salvelinus namaycush*) embryos in an acidified lake in northwestern Ontario. Can. J. Fish. Aquat. Sci. 47: 236–243.

Survival and development of lake trout (*Salvelinus namaycush*) embryos from L223 in the Experimental Lakes Area, northwestern Ontario, were evaluated from 1979 (pH 5.6) to 1982 (pH 5.1). Survival of L223 embryos was not significantly correlated to lake pH during experimental acidification. Also, embryo mortality in L223 was not significantly different from that of lake trout embryos in two reference lakes, L224 and L468. Survival of L223 embryos was not improved when they were incubated in nonacidified lakes. Embryo mortality was highest in all lakes (33–81%) within 15 d of fertilization. Mortality was negligible from Day 15 until the termination of the seasonal observations (Day 120 or 150). High variability in embryo survival existed between individual females within a single lake. The mean size of eggs from L223 lake trout decreased significantly from 1979 to 1982. Recruitment failures occurred in L223 from 1980 to 1982. We hypothesize that lake trout recruitment failure in L223 occurred between the posthatching period (spring) and actual recruitment into the population as young-of-the-year (fall) and that embryo mortality in this lake was not critical to population recruitment.

La survie et le développement d'embryons de touladis (*Salvelinus namaycush*) du lac L223 dans la Experimental Lakes Area (zone de lacs expérimentaux) du nord-ouest de l'Ontario, ont été évalués entre 1979 (pH 5,6) et 1982 (pH 5,1). La survie des embryons du L223 n'a pas présenté de corrélation significative avec le pH du lac au cours de l'acidification expérimentale. De plus, la mortalité des embryons dans L223 n'était pas significativement différente de celle des embryons de touladis dans deux lacs de référence, L224 et L468. La survie des embryons de L223 n'a pas été améliorée lorsqu'ils ont été incubés dans des lacs non acidifiés. La mortalité des embryons était la plus élevée dans tous les lacs (33–81%) dans les 15 d suivants la fertilisation. La mortalité était négligeable du jour 15 jusqu'à la fin des observations saisonnières (jour 120 ou 150). Les femelles d'un seul lac ont présenté une grande variabilité dans la survie des embryons. La taille moyenne des oeufs du touladi du L223 a diminué de façon significative entre 1979 et 1982. Dans L223, un échec du recrutement a été observé entre 1980 et 1982. Nous posons l'hypothèse que l'échec du recrutement de touladis dans L223 a lieu entre la période suivant l'éclosion (printemps) et l'arrivée dans la population sous forme de jeunes de l'année (recrues à l'automne) et que la mortalité des embryons dans ce lac n'a pas d'effet sur le nombre de recrues.

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The acidification of many North American freshwater lakes and rivers has led to the extinction of many indigenous fish populations (Beamish 1974; Beamish et al. 1975; Schofield 1976; Harvey and Lee 1982). Reduced population size has usually been due to decreased recruitment into the population rather than to increased adult mortality (Beamish 1974; Haines 1981). However, in some extreme instances increased adult mortality may also be a contributing factor (Rossland et al. 1986; Mills et al. 1987).

Recruitment failures in acid-stressed lakes have been attributed to several sensitive processes, i.e. decreased egg production (Craig and Baksi 1977; McCormick et al. 1980), increased embryonic and/or fry mortality (Beamish 1974; Leivestad et al. 1976; Schofield 1976; Daye and Garside 1977; Lacroix 1985; Hunn et al. 1987; Mount et al. 1988), and increased posthatching mortality (Trojnar 1977; Daye and Garside 1977; Van Winkle et al. 1986; Gunn 1986). In general, the order of sensitivity to acid stress is thought to be egg production, fry survival, fry and embryonic growth, and egg fertility (Zischke et al. 1983).

Gunn (1986) suggested that for lake trout (*Salvelinus namaycush*) the most sensitive period is immediately following hatching when the fry are vulnerable to depressed-pH spring runoff. Kennedy (1980), on the other hand, reported many embryological failures shortly after egg fertilization (within 15 d) in an acid-stressed (pH 5.8) lake trout population and predicted subsequent recruitment failures. However, sensitivity to low pH varies among species and among individuals of one species (Mount et al. 1988). Lacroix (1985) stated that critical pH levels were often site specific and related to ambient water quality.

We initiated this study in 1979 to confirm the initial results of Kennedy (1980) for lake trout from acidified Lake 223 of the Experimental Lakes Area and to determine whether we could correlate population recruitment failures, as indicated by both the Jolly-Seber model and catch-per-unit-effort (CPUE) (Mills 1984; Mills et al. 1987), with increased mortality of lake trout embryos in this lake. We addressed three individual

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TABLE 1. Mean open-water epilimnetic pH values for Lakes 223, 224, and 468 prior to and during experimental acidification of L223. A: Mean open water epilimnetic pH, B: pH on Day 0 of experiment (day of fertilization), C: time weighted mean pH for whole incubation period (Day 0 to 150).

		Year									
Lake		1973	1974	1975	1976	1977	1978	1979	1980	1981	1982
L223	A	7.0	6.7	6.6	6.5	6.1	5.9	5.6	5.6	5.0	5.1
	B							5.5	5.1	5.2	5.1
	C							5.9	5.3	5.3	5.2
L224	A	7.1	6.6	6.7	6.6	6.5	6.8				6.8
L468	A	7.0					7.0				7.1

hypotheses: (1) mortality of eggs in incubators was linked to year class success in an acidified lake, (2) mortality of eggs in incubators was directly correlated with level of acidity, and (3) if (2) occurred then increased mortality would occur between the egg stage and the swim-up fry stage. With respect to the latter, we felt that identifying the most sensitive stage of embryonic development could be useful in designing short-term amelioration strategies such as liming.

Materials and Methods

Lake trout eggs were obtained from three different populations in the Experimental Lakes Area, northwestern Ontario (Cleugh and Hauser 1971): Lake 223 (L223), Lake 224 (L224), and Lake 468 (L468). Lake 223 had been experimentally acidified starting in 1976 (pH 6.7) (Cruikshank 1984); this continued through the duration of this study with a targeted pH value of 5.0 for 1982 (Schindler et al. 1985). Lakes 224 and 468 were natural, undisturbed lakes used as references. During this study the open-water mean epilimnetic pH in L223 decreased from 5.6 in 1979 to 5.1 in 1982; in L224 and L468 the open-water mean pH was stable at approximately 6.8 and 7.1, respectively (Table 1). The pH in L223 at the time of egg fertilization (early October) decreased from 5.5 in 1979 to 5.2 in 1982 (Table 1). Mean pH values throughout the egg-incubation period were somewhat higher and ranged from 5.9 in 1979 to 5.2 in 1982 (Table 1). All three lakes were oligotrophic, dimictic lakes which stratify during the summer months. Each contained self-sustaining, unexploited lake trout populations prior to any experimentation (Mills et al. 1987).

Eggs and sperm were collected from adult lake trout captured during peak spawning periods on or near spawning beds in each lake using trap nets, gill nets, and angling. Fish were anaesthetized using tricaine methanesulfonate (MS222) and fork length and weight measurements were recorded (Table 2). Only ripe and running females, those which readily released their eggs, were used in this study. Eggs from these females were placed in spawning trays containing approximately 200 mL of ambient lake water. Eggs were then fertilized using the milt from several ripe males. The fertilized eggs were left undisturbed and hardened for 4 to 12 h after which nonviable eggs (those which had turned a milky white colour) were removed. Also, subsamples of fertilized eggs were removed to the lab and used to determine egg size by volume displacement. Egg volumes were converted to diameters using standard conversion equations for spherical objects.

Following the hardening period, eggs were carefully placed into clear plexiglass incubators (Fig. 1), modified slightly from those used by Kennedy (1980). In 1979 and 1980, eggs from each of six individual females per lake were separately fertilized, held, and then placed into separate incubators. A "set" of incubators consisted of six individual incubators, each containing eggs from an individual female. In 1981 and 1982, eggs from all females were pooled in each lake, fertilized, and then randomly placed into all incubators of each set. The number of sets of incubators in each lake corresponded to the number of sampling periods in each year ($N=4$ in 1979 and 1980; $N=5$ in 1981 and 1982).

Each plexiglass incubator held 30 eggs in individual cells. Each cell was 13 mm in diameter and 13 mm deep. Each incubator was permanently backed by plasticized nylon mesh screen and had a hinged plexiglass-reinforced, nylon mesh front. Sets of incubators consisted of six incubators attached to a plexiglass bar using galvanized eyelets (1979, 1980) or by spot gluing (1981, 1982). Sets were then suspended in the water column at a depth of 2 to 3 m. The incubators all hung vertically in the water, approximately 0.2 to 0.5 m above the lake bottom. Floats and anchors secured the sets of incubators in this position throughout the incubation period (Fig. 1).

We placed sets of incubators in the lakes near known lake trout spawning areas. Lake 223 and lake 224 eggs were incubated in each lake, respectively, from 1979 to 1982. Lake 468 eggs were incubated in L468 in 1982. Commencing in 1981, additional incubator sets were exchanged between the three lakes. Lake 223 eggs were incubated in L224 in 1981 and 1982. Lake 224 eggs were incubated in L223 in 1982 and L468 eggs were incubated in L223 in 1982. All eggs were water hardened and transported in water from the lake of origin. Upon reaching the destination lake, the eggs were allowed to settle. All, if any, damaged eggs (opaque) were then removed prior to placing the incubators in the water column.

The start and duration of the lake trout spawning period varies from lake to lake and from year to year in the same lake at the ELA. In order to compare data from several years, the date of artificial egg fertilization for each year in each lake was designated as Day 0. Subsamples of 30 fertilized eggs (one incubator from each set) were then analyzed on approximately Days 15, 60, 90, 120, and 150 of incubation. The total number of eggs still alive in each incubator was recorded, and all eggs, both alive and dead, were preserved using Davidson's solution. Development of the live embryos was visually assessed according to criteria of Kennedy (1980). Total lengths of embryos were also determined using both microscope micrometers and measuring tape.

Numbers of surviving eggs were originally expressed as a percentage of total eggs in each incubator. An angular trans-

TABLE 2. Mean fork lengths (FL) (mm), weights (wt) (g), and condition factor (K) of female lake trout from Lakes 223, 224, and 468 used in this study. Values prior to 1979 are means from all mature females sampled during the spawning season. Values in parentheses are standard deviations.

		Year					
Lake		1976	1978	1979	1980	1981	1982
L223	FL	421 (24.3)	434 (21.3)	441 (18.2)	430 (20.1)	415 (26.0)	407 (51.5)
	Wt	958(215.0)	1011(162.8)	974(135.2)	839(144.2)	753(116.5)	705(257.0)
	K	1.284	1.237	1.136	1.055	1.053	1.046
L224	FL	369 (20.0)	421 (24.3)	388 (15.8)	405 (13.7)	385 (12.6)	383 (15.7)
	Wt	559(110.7)	630(108.5)	639 (71.7)	768 (89.1)	621(139.4)	633(152.6)
	K	1.113	0.844	1.094	1.156	1.088	1.127
L468	FL	—	—	—	—	—	429 (3.2)
	Wt	—	—	—	—	—	937(100.5)
	K	—	—	—	—	—	1.187

formation (arc-sin, square root) was conducted on the data prior to statistical analysis (Snedecor and Cochrane 1980). Variation between females, years, and lakes were assessed using a two-way classification model of analysis of variance with replication. Least squares differences (LSD) was used to test significance of individual sample means. Significant differences were evaluated at a 95% probability level. Because of the occasional loss of individual or sets of incubators, an unequal sample size model was used in some calculations.

Results

Embryo Survival

Survival of embryos incubated in the lake of origin varied significantly from year to year (Fig. 2). Embryo survival in L223, the acidified lake, was highest in 1980 (59.8%) and lowest in 1981 (34.8%). However, the mean value in 1979 was not statistically different from the mean value in 1982. Embryo survival in Lake 224 differed significantly from year to year; the highest value was recorded in 1982 (63.0%) and the lowest (18.7%) in 1981. No significant correlation existed between percent embryo survival and lake pH for either Lake 223 or Lake 224.

Embryo survival was also compared between acidified L223 and nonacidified L224 and L468. The mean annual survival of embryos from L223 did not differ significantly from that of embryos from L224 in 1979 and 1980 (Fig. 2). In 1981, L224 embryo survival was significantly lower, by approximately 50% (LSD-test), than L223 embryo survival. In 1982, L224 embryo survival was 28% higher than survival of L223 embryos and 23% higher than L468 embryos (both significant; LSD-test). Lake 223 and L468 embryo survivals were not significantly different from each other in 1982.

Embryo mortality in all lakes and years was highest between Day 0 and 15. During this period, average mortality ranged from 37 to 63% in L223 and from 33 to 81% in L224 (Fig. 3). In 1979, 1980, and 1981, L223 embryo survival did not change significantly from the first sampling period (Day 15) to the final sampling period (Day 120). In 1982, embryo survival in L223 was much lower at Day 120 (28.9%) than at any other time in that year (mean = 53.8%). This is likely an anomalous result because survival at Day 150 was similar to that at prior samplings on Days 15, 60, and 90. In L224 and L468, embryo survival also remained relatively constant from the first to the last samplings in all years of the study (Fig. 3).

In 1979 and 1980, survival of embryos from individual female lake trout was evaluated. In both years, mean survival of embryos from different females in their respective lakes differed significantly (Table 3). In L223, mean survival ranged from as low as 32% to as high as 85% for individual females. In L224 the results were even more extreme, with embryo survival ranging from 0 to 93%. In 1981 and 1982, fertilized eggs from individual females were pooled prior to placement in the incubators to improve lake to lake comparisons. Two way analysis of variance for 1981 and 1982 data indicated no significant difference between incubators containing pooled eggs from all females.

Transplant Experiment

In 1981 and 1982, eggs from acidified Lake 223 were incubated in the two reference lakes, L224 and L468 (1982 only). In 1981, the mean survival of L223 embryos that were incubated in L224 was 46.9%, significantly higher than the survival of all embryos incubated in their lakes of origin (Fig. 2). In 1982, eggs from L223 incubated in L224 had a mean survival of 59.2% while those incubated in L468 had a mean survival of 47.1%. Survival of L223 embryos incubated in the two reference lakes in 1982 was not significantly different from the mean survival of other embryos incubated in their lake of origin (Fig. 4). Survival of the transplanted L223 embryos was consistently higher during the early stages of the incubation (<Day 90); by Day 120, survival of transplanted embryos was similar to that of resident embryos.

Lake trout eggs from L224 and L468 were also incubated in L223 in 1982; in both instances, the mean survival of the reference lake embryos was lowered significantly by incubating them in the acidified lake (Fig. 4). Interestingly, the survival of embryos from both reference lakes, when incubated in L223, did not differ significantly from the survival of resident incubated L223 embryos (LSD-test; $P>0.05$) (Fig. 4). The highest embryo mortalities in the transplant experiments occurred between Day 0 and 15. Survival was relatively constant throughout the remainder of the incubation period.

Embryo Growth and Development

Fertilized eggs from L223 were consistently smaller (mean egg diameter) than eggs from both reference lakes ($P<0.05$)

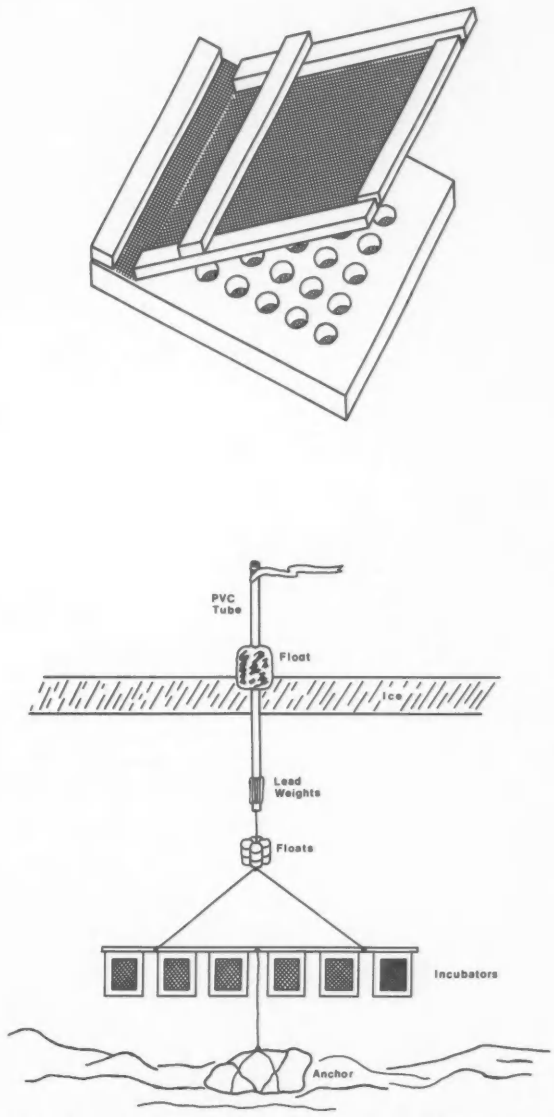

FIG. 1. Schematic diagram of incubator setup used in lake trout experiment in all lakes, 1979 to 1982.

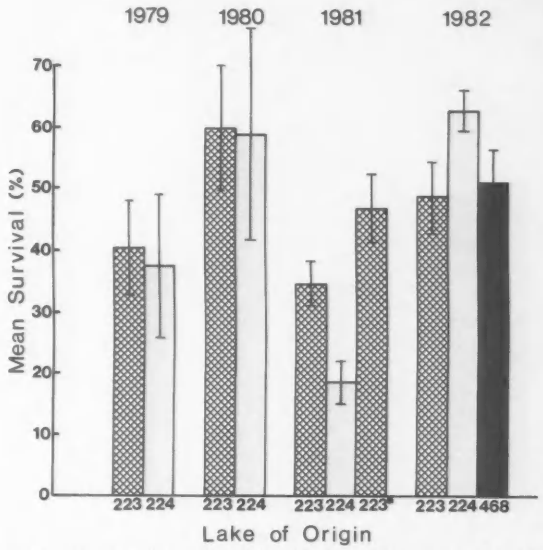

FIG. 2. Mean yearly survival (%) of lake trout embryos incubated in the lake of origin from 1979 to 1982. Ninety-five percent confidence intervals are shown. "223*" indicates L223 eggs incubated in L224.

(Table 4). At the same time the mean size (fork length and weight) of female lake trout in L223 was larger than those from L224 and similar to those from L468 (Table 2). The mean egg diameter in L223 decreased from 1979 to 1982 while no notable change in mean egg diameter occurred in the two reference lakes (L224 and L468). The reduction in egg size in L223 was positively correlated ($r^2 = 0.824$) with a significant decline in L223 fish condition (Mills et al. 1987) and weight during the same time period (Table 2). Fish condition and egg diameter did not change significantly in L224 from 1979 to 1982.

Embryo length was not significantly different between L223 and L224 in 1979 (LSD-test; $P > 0.05$) (Fig. 5). In all subsequent years, embryo length in L224 and L468 exceeded that in L223 (LSD-test; $P < 0.05$) (Fig. 5). Mean length of embryos in both L223 and L224 increased significantly from 1979 to 1982. However, the rate of growth of embryos from all three lakes was linear with time; no significant differences in rate of growth (slope of regression) occurred between the lakes (Fig. 5).

Development of lake trout embryos was also monitored in the viable eggs from each sampling period during the experiment. The rate of embryo development appeared to be similar in all three lakes throughout the study. Notochord development was evident at Day 15 and by Day 60 most of the embryos were at an early eyed stage. By Day 120 of the incubation all embryos from all lakes had hatched as sac fry. In all years of this study live embryos showed no signs of external deformity or abnormal swimming behavior. Postmortem examination of dead embryos was not conducted.

Discussion

The lake trout population in Lake 223 began to experience recruitment failure in 1980 when the pH of the lake reached 5.6 (Mills et al. 1987). This pH is within the range 5.6 to 5.1, generally accepted as critical to lake trout recruitment failures (Schofield 1982; Beggs and Gunn 1986; Mills et al. 1987). At that time, fish were still spawning although no young-of-the-year lake trout were seen after 1979. However, the results from our study indicate continued viability of lake trout eggs and survival of embryos throughout this period of little or no recruitment. Therefore, we rejected the hypothesis that mortality of eggs in incubators is related to year class success in an acidified lake.

Survival of Lake 223 eggs and embryos did not decrease with time as the pH of the lake was reduced; in fact mean embryo survival was slightly higher in 1982 than in 1979. There was no direct correlation between egg mortality in Lake 223 and the level of acidity in the lake. Also, lake trout egg and embryo survival did not differ among the three lakes in 1979, 1980,

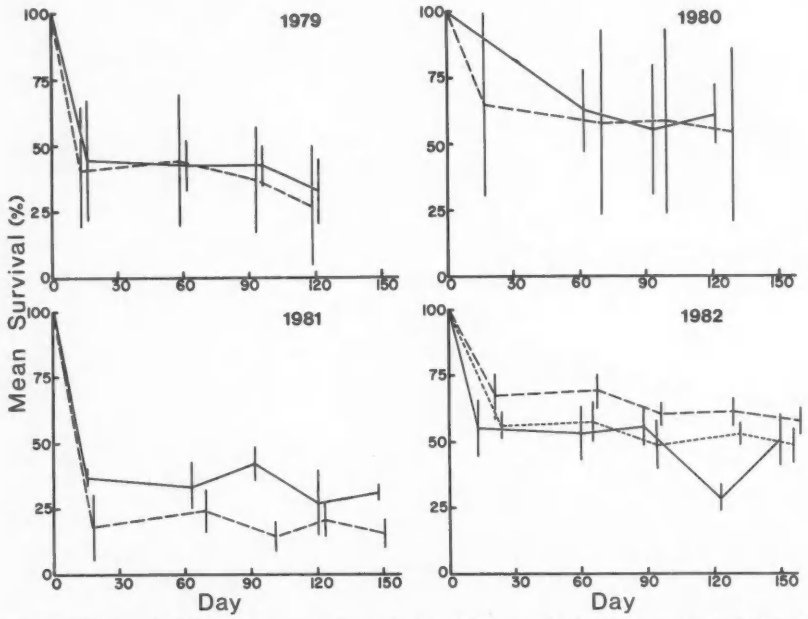

FIG. 3. Mean survival (%) of lake trout embryos in Lake 223 (—), Lake 224 (– –), and Lake 468 (....). Ninety-five percent confidence intervals are also shown.

TABLE 3. Mean lake trout embryo survival for six individual females from Lake 223 and Lake 224, 1979 and 1980.

		Female					
Lake	Year	1	2	3	4	5	6
L223	1979	43.4	55.4	31.7	30.8	—	—
	1980	80.0	42.2	47.8	84.5	53.3	51.1
L224	1979	9.2	42.5	68.8	41.7	2.5	60.0
	1980	83.3	93.3	86.7	6.7	83.8	0.0

and 1982; in 1981, Lake 223 egg survival was higher than in one reference lake and lower than in the second reference lake. We therefore rejected the hypothesis that embryo survival was directly affected by pH values greater than 5.0 and concluded that egg mortality was not directly related to year class failures in L223. This finding is consistent with Carrick (1979) who found that a pH greater than 4.5 has no obvious effect upon hatchability of eggs from brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*).

Embryo survival did not change when we incubated eggs from the acidified lake in the reference lakes. However, survival of eggs and embryos from the reference lakes was reduced when incubated in the acidified lake. Low pH in L223 may therefore have been detrimental to eggs from other lakes but not to egg and embryo development of resident L223 lake trout. We hypothesize that the eggs and embryos from L223 became more resistant to the low pH values in that lake, a trait most probably inherited either physiologically or selectively from the spawning adults. Gunn (1986) also suggests that factors such as acclimation and body energy reserves may affect the response of fishes to low pH.

Several studies have indicated that mortality of fish eggs and/or embryos occurs somewhere between fertilization and larval swim-up stage (Daye and Garside 1977; Trojnar 1977; Rombough 1982). In our study, embryo mortality occurred during two distinct periods. Mortality first occurred immediately following fertilization, when the egg is undergoing active water uptake and hardening, making it highly vulnerable to external environmental conditions (Lee and Gerking 1980). Initial high mortality recorded in Lake 223 was also observed in the two nonacidified lakes. We therefore conclude that the initial high mortality was not a function of low pH values.

Initial high mortality values were more likely a function of the high variability among egg and embryo survival results obtained from individual females. In 1979 and 1980, embryo survival calculated for individual females ranged from 30 to 85% in L223. Similar variability was also observed in the nonacidified reference lakes. Therefore, we feel that the high variability among females was not acid induced. Lake trout have been known to develop normal eggs during the spawning period, not spawn, and then resorb the eggs (Balon 1980). If females resorbing eggs were combined with normally spawning females, the results could be similar to those recorded in our study.

The extreme degree of variability observed between females in this study may explain the difference between our results and those of Kennedy (1980). Kennedy (1980) observed extreme mortality and teratogenesis in eggs from acidified L223 and very little mortality in the reference lake, L224; however, Kennedy used only one female from each lake. Our results from 1979 and 1980 suggest that this approach was inappropriate because of the high variability in egg survival found among different females.

The consistency of the survival rates following the first 15 d of incubation indicate little or no mortality during this devel-

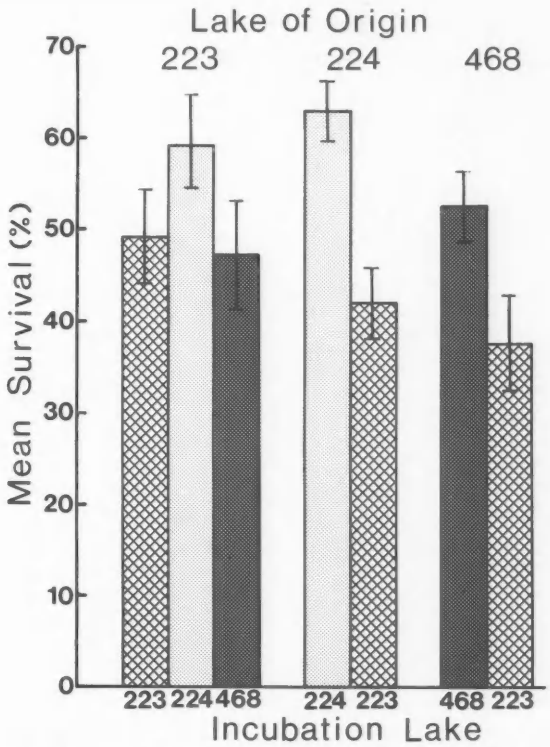

FIG. 4. Mean yearly survival (%) of lake trout embryos, 1982, incubated in lakes of origin and reference lakes. Ninety-five percent confidence intervals are also shown.

TABLE 4. Mean diameter (mm) of Lakes 223, 224, and 468 lake trout eggs taken immediately following fertilization. Values in parentheses are standard deviations.

	Lake		
Year	223	224	468
1978	5.60(0.12)	5.92(0.21)	—
1979	5.61(0.22)	6.08(0.33)	—
1980	5.49(0.29)	6.16(0.28)	—
1981	5.38(0.23)	6.03(0.28)	6.60(0.20)
1982	5.41	5.97	6.56
1983	—	5.90(0.15)	6.45(0.21)

opment period of the embryos. At this time the embryo is in the early and advanced eyed stage, encapsulated within the outer egg covering which provides protection against external environmental factors. It is at this stage that the embryo is the most resistant to acidic conditions (Daye and Garside 1977; Rombough 1982; Beggs et al. 1985).

Lake trout fry become more sensitive to low pH as sac fry and larvae (Daye and Garside 1977; Gunn and Keller 1984). This period of sensitivity usually coincides with spring acid pulses caused by snowmelt runoff. In our study, lake trout hatched as sac fry between 90 and 120 d following egg fertilization. However, these newly hatched larvae were not exposed to low pH snow melt in L223 and survival did not change significantly during this period in any of the lakes we studied.

The second period of increased mortality of lake trout fry in Lake 223 may occur sometime between ice-off (posthatching; last sampling period) and the time at which trout fry were recruited into the population the following fall. Lake trout survival was monitored for up to 150 d following fertilization with no indication of increased mortality other than that observed immediately following spawning. However, the absence of fingerlings in the lake indicates the loss of these potential recruits sometime between swim-up and active recruitment into the population.

The production of eggs by female lake trout in Lake 223 did not change throughout this study nor did the rate of egg resorption by females change (Mills et al. 1987). This is similar to results obtained under acid-stress laboratory conditions by Mount et al. (1988) for brook trout (*Salvelinus fontinalis*). The average size of the L223 eggs and the condition of mature lake trout did decrease (Mills 1984) as the pH decreased in this lake, an indication of stress on the mature fish. More important, however, is the fact that the smaller L223 eggs and embryos had the same egg survival and rate of development as the eggs and embryos from the two reference lakes. This information tends to support our hypothesis that recruitment loss occurred sometime after larval hatching.

We hypothesize several causes for increased lake trout larval mortality in L223. First, lake trout offspring may have acquired a sensitivity to low pH from the parental stock and the stress was therefore "carried-over" to the recruitment class. This phenomenon has been described by Mount et al. (1988) where the exposure of adults to stressful conditions decreases the resistance of their offspring to the same stressful conditions. Sensitivity may have been greater once the embryos hatched, leaving the protective environment of the egg capsule. Other factors causing reduced recruitment include pH induced chemical imbalances in the lake (i.e. Ca decreases, Al increases), loss of available food resources, or increased predation by adult lake trout. Lacroix et al. (1985) concluded that emergent Atlantic salmon fry survival was significantly reduced at pH 5.0 by starvation. This may have occurred in Lake 223. Dramatic changes in the biotic community in Lake 223 (Schindler et al. 1985; Mills and Schindler 1986) may have reduced the available food supply for the exogenetic feeding larval lake trout. We conclude, therefore, that pH values less than 5.6 indirectly rather than directly led to recruitment failures in Lake 223. Loss of recruitment occurred sometime between the posthatching stage and the fingerling stage the following fall. Further research is necessary to determine which, if any, physiological or biological stresses are involved in the mortality of lake trout during this period.

Acknowledgments

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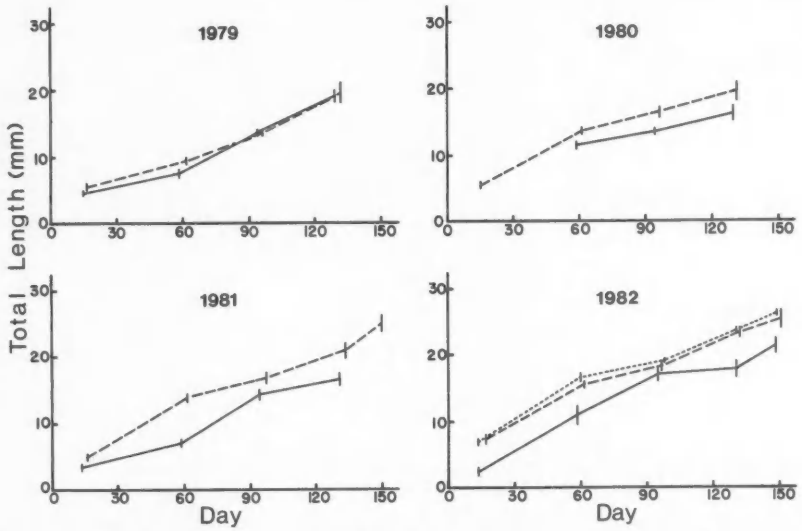

FIG. 5. Growth of lake trout embryos from Lake 223 (—), Lake 224 (– –), and Lake 468 (....), from 1979 to 1982. Ninety-five percent confidence intervals are also shown.

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Application of Removal Sampling to Estimate the Density of Ringed Seals (*Phoca hispida*) in Barrow Strait, Northwest Territories

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The density of ringed seals (*Phoca hispida*) in 2 to 4 km^2 study plots was determined using a combination of removal sampling to determine density of seal holes and estimates of hole to seal ratios. A dog survey technique was adapted to removal sampling, where seal holes located under the snow by the dogs during surveys of fixed effort were marked and treated as removals from the population. Computer simulation indicates that estimates of seal hole density are within 10% of the true population size if for each plot there are ≥ 4 searches, sampling intensity is ≥ 0.85, the coefficient of variation of the estimate is ≤ 0.3, and the probability of detecting a seal hole is ≥ 0.35. The quality of survey results was affected by the number of dogs used to survey each plot, plot size, and surface topography. Densities of seal holes varied from 4.8 to 7.9 holes·km^{-2}. Eight seals had an average hole to seal ratio of 3.4. Seal densities ranged from 1.4 to 2.3 seals·km^{-2}, and may be much higher if pup production is included.

Le nombre de phoques annelés (*Phoca hispida*) dans les quadrats d'études a été déterminé à l'aide d'une combinaison d'échantillonnage par enlèvement pour déterminer la densité des trous de phoques et estimer le ratio de ces derniers. Une technique de repérage à l'aide de chiens entraînés est adaptée pour l'échantillonnage par enlèvement. Les trous de phoques sont localisés sous la neige au cours de séances de recherche à effort constant, puis marqués et considérés comme enlevés de la population. Une simulation sur ordinateur indique que l'estimation de la densité des trous de phoques est à l'intérieur de 10% de la grandeur de la population actuelle. Si pour chaque quadrat il y a ≥ 4 recherches, l'intensité de l'échantillonnage est $\geq 0{,}85$, le coefficient de variation de l'estimé est $\leq 0{,}3$, et la probabilité de trouver un trou de phoque est $\geq 0{,}35$. La qualité des résultats de repérage est affectée par le nombre de chiens utilisés pour dépister chaque quadrat, la grandeur des quadrats et la topographie du terrain. La densité des trous de phoque varie de 4,8 à 7,9 trous·km^{-2}. Huit phoques sont un ratio de 3,4 trous·km^{-2}, et peut-être plus élevé si les jeunes phoques sont inclus.

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Censuses of ringed seal, *Phoca hispida*, populations in fast ice are hampered by their use of subnivean lairs (McLaren 1958). One approach has been to fly aerial surveys after the lairs have melted and count the number of seals hauled out on the ice during the spring moult (Stirling et al. 1977; Kingsley 1984; Kingsley et al. 1985). Aerial surveys cover large areas in a short time, but because not all seals are on the ice they underestimate total population size. Also, major changes in survey results may reflect changes in the proportion of hauled out seals and not real changes in seal numbers (Smith and Hammill 1981; Kingsley 1984).

An alternative approach has been to conduct ground surveys during the March to May whelping period. Trained dogs running in front of a snow machine, locate the subnivean holes of the ringed seal (Smith and Stirling 1975, 1978). Seal abundance is expressed as the number of minutes searched per seal hole located. This method provides important information on mortality from predation, annual production, and population composition. However, the dog search technique provides only an index of hole abundance, which is still only an index of seal abundance. Further, it is not possible to determine whether the dog has detected all seal holes in the area surveyed or whether the proportion of detected (or undetected) holes is the same for various survey conditions or different dogs. Dog searches have been used extensively in studies of the fast ice ecology of the ringed seal, but these shortcomings have never been examined.

We might assess variability in detection abilities within or between dogs by repeatedly surveying the same area under different conditions. Unfortunately, experienced dogs make extensive use of visual clues such as polar bear tracks, but ignore seal holes they visited previously. Ringed seals also tend to be sensitive to activity on the ice because of predators (Smith 1976, 1980). Repeated surveys over several days cause animals to abandon holes which may not be reoccupied during subsequent surveys.

One method of overcoming some of the problems associated with the dog survey technique is to adapt the dog survey to an established sampling procedure that allows the total number of seal holes in the population to be estimated. Here we examine the application of a catch per unit of effort model called the

removal method (Moran 1951; Zippin 1956, 1958) to dog survey data, to estimate the number of seal holes in study plots located in Barrow Strait between 1984 and 1986. We also apply hole to seal ratios to estimate seal density in their breeding habitat.

Model Development

The removal method was originally developed for use in small mammal studies where the animal is trapped and permanently removed from the population (Moran 1951; Zippin 1956, 1958; Seber 1982). If trapping effort remains constant, then the population size (N) can be estimated from;

$$(1)\quad N = Y\cdot(1-q^k)^{-1},$$

where Y is the total number of animals trapped, q is the probability that an animal will not be caught during a single trapping period and k is the number of trapping periods. A solution for q is determined by solving the equation;

$$(2)\quad q\cdot p^{-1} - (k\cdot q^k)\cdot(1-q^k)^{-1} = \left[\sum_{i=1}^{k}(i-1)\cdot y_i\right]\cdot Y^{-1},$$

where $p=(1-q)$ is the probability of an animal being trapped and y_i is the number of animals trapped during the ith trapping period ($i=1, 2, \ldots k$).

The variance of N is estimated by;

$$(4)\quad V(N) = N\cdot(1-q^k)\cdot[N(-F')(1-q^k) - (k\cdot p)^2\cdot q^{-1}]^{-1} \text{ where}$$

$$(5)\quad F' = -N^{-1}[(1-q^k)\cdot q^{-k} - (1-q^{2k})\cdot(2\cdot N\cdot q^{2k})^{-1} + (1-q^{3k})\cdot(6\cdot N^2\cdot q^{3k})^{-1}]$$

and 95% confidence limits are estimated by $\pm$ 1.96 $(V(N))^{0.5}$.

The likelihood function cannot be maximised unless a decline occurs in y_i as k increases (Otis et al. 1978). If subsequent trapping does not cause a decline in population size then the iterative solution of equation (2) will not converge. Conditions for the experiment to fail are given by;

$$(3)\quad \sum_{i=1}^{k}(k+1-2\cdot i)\cdot y_i < 0 \text{ (Seber 1982).}$$

In our application of the removal method we consider the detection of a seal hole by the dog as a removal. Each time the dog locates a new seal hole it is marked with a small numbered stake and removed from the population of seal holes in that plot. We replace trapping effort by search effort defined as total time spent searching for seal holes by the dog.

The remaining terms of the removal method are redefined as follows; k is the number of search periods completed at each plot; p is the probability of the dog detecting a seal hole during a search; y_i is the number of new seal holes discovered during each search period ($i=1,2\ldots k$) and Y is the total number of seal holes located by the dog in the plot

$$\left(Y=\sum_{i=1}^{k} y_i, \text{ where } i=1, 2, \ldots k\right).$$

In a population survey an accurate estimate is one in which the difference between the estimate and the true population size is quite small. Robson and Reiger (1964) considered an accuracy of $\pm$25% to be adequate for management studies, but an accuracy of $\pm$10% is necessary for careful research into population dynamics. The precision of an estimate is assessed by the width of the 95% confidence interval. This interval must be wide enough to encompass the true population size 95 times out of 100, but must not be so wide so as to cast doubt on the population estimate (Roff 1973a). In order to obtain an accurate and precise estimate it is necessary that the assumptions underlying the model used in the estimation procedure are satisfied.

In using the removal method to estimate seal hole density we assume that the population of seal holes is closed, the probability of the dog detecting a seal hole is the same for all holes, remains constant between searches, the detection of seal holes is independent, and search effort in the plot remains constant.

Seal holes may be abandoned because of our activity on the ice or new holes might be created, violating the closure assumption (Hammill and Smith 1989). To counteract this possibility, our searches were completed in as short a time as possible, usually within 2 to 3 d.

The assumption that all holes are equally likely to be detected is the most difficult to satisfy. Zippin (1956) proposed that departures from this assumption, be tested by;

$$(6)\quad \chi^2 = \sum_{i=1}^{k}[y_i - (Y\cdot p\cdot q^{i-1})\cdot(1-q^k)^{-1}]^2\cdot[(Y\cdot p\cdot q^{i-1})\cdot(1-q^k)^{-1}]^{-1}$$

but Roff (1973b) cautions that these tests are insensitive. We conducted a computer simulation in which the probability of detecting a seal hole varied randomly between searches. Our objective was to determine if the Chi-square goodness of fit test (Zippin 1956) detected departures from the assumption of equal probability of detection. Secondly, could information obtained as part of the estimation or sampling procedure be used to determine if an estimate was valid.

Materials and Methods

Simulation

The removal model was applied to a simulated population (N) of 10, 20, and 40 seal holes. Three to six removals or draws without replacement (k) were made from each population. The proportion of simulated seal holes removed during each trial varied randomly between draws. One hundred simulations were conducted for each combination of k and N for a total sample size of 1200. We defined a valid estimate as one in which the 95% confidence interval bracketed the true population size 95 times out of 100 and if the estimate had an accuracy of $\pm$10% of the true population size. Accuracy was measured by error where; error $=(N-\hat{N})\cdot N^{-1}$. $\hat{N}$ is the population estimate and N is the true population size. We also calculated the coefficient of variation of the estimate as the ratio between the standard error of the estimate and the estimate, and sampling intensity. Sampling intensity is the number of holes detected during the simulations divided by the estimated population size. We used estimated population size because in a field study the true population size will not be known.

Field Surveys

The initial study area of 3100 km^2 lay between Lowther and Griffith Islands in the north and Russell and Somerset Islands in the south (Fig. 1). Normally this area is covered by first year fast ice, which beings to form in November and remains in place until July (Lindsay 1975, 1977). In 1984 and 1985 normal ice formation and breakup patterns were observed, but in 1986 our study area did not freeze over. We extended the study area northwards to McDougall Sound and south into Peel Sound (Fig. 1).

FIG. 1. Location of study plots surveyed in Barrow Strait, Northwest Territories. Plots 1–9 were surveyed in 1984 and 1985. Plots 10–23 were surveyed in 1986. The dotted line represents the fast ice edge in 1986.

Densities of seal holes were estimated in 4.0 km^2 (plots 1–9) in 1984 and 1985 and 2.25 km^2 study plots (plots 10–23, Fig. 1) in 1986. Plots were located on the sea ice by snowmobile using a satellite navigation system (Magnavox MX4102, Torrance, California, USA).

Seal holes were located under the snow by trained Labrador retriever dogs (Smith and Stirling 1975). In 1984, two dogs were used in the surveys. Each dog searched a plot once a day for 40 to 70 min. In 1985 and 1986, only one dog was used. This dog ran twice daily for 30- to 40-min search periods.

The dog ran transects lying perpendicular to the wind direction. Searches began at the downwind end of the plot and moved upwind as the dog detected seal holes. The same transect was not reestablished after the dog detected a hole. Instead the dog continued running across the wind from the most recently detected seal hole until the boundary of the plot was reached. If time remained after the dog had reached the upwind end of the plot then the dog was taken to search areas in the plot that had been missed in earlier passes in that session.

We also measured windspeed, air temperature, mean snow depth, and ice deformation to determine their effects on the dog's ability to detect seal holes (Hammill and Smith 1989).

In March and April if a seal does not return to a breathing hole within 12 h a thin layer of ice 1–2 cm thick forms. We determined hole to seal ratios by killing a seal at its breathing hole and then checking previously identified holes and new holes found during subsequent surveys for freezing. Holes covered by a thin layer of ice were assumed to have been occupied by the seals that we removed.

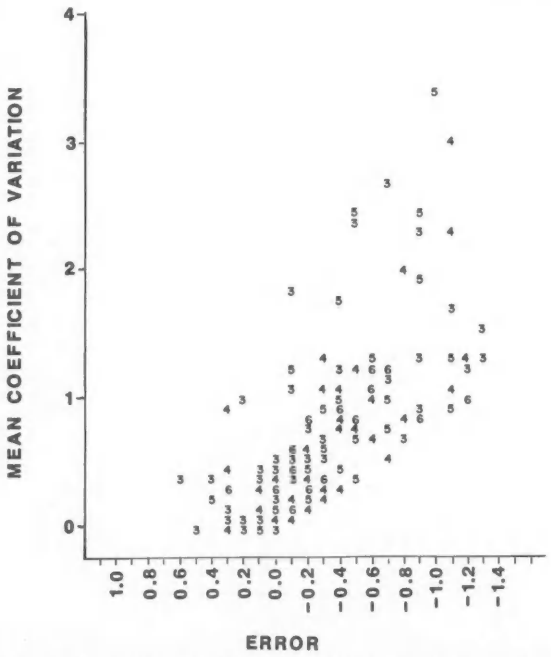

FIG. 2. Plot of mean coefficient of variation against error, where error $=(N-\hat{N})\cdot N^{-1}$. Numbers plotted on the graph represent values for number of searches (k).

Differences between means were tested by analysis of variance. Statistical procedures were completed using PROC, CORR, and PROC GLM on the PC-Statistical Analysis System (SAS Institute 1985).

Results

Simulation

A solution was not obtained for one trial because the data did not satisfy the failure criterion given in equation (3).

In the simulation experiment, the chi-square test was not effective in detecting violations of the assumption of equal probability of detecting seal holes. Sixty-two percent of 1199 simulations had nonsignificant chi-square values, but the 95% confidence interval encompassed the true population size in only 51% ($N=384$) of the trials. Sixteen percent of the trials produced estimates with an error >10%, while 60% of the estimates rejected by the chi-square test differed from the true population size by <10%.

We investigated the feasability of using coefficient of variation, sampling intensity, and probability of detecting a seal hole to determine if threshold values for these statistics would indicate if an estimate was within 10% of the true population size. Accurate estimates could not be detected using only the coefficient of variation. A strong positive correlation between the population estimate and its coefficient of variation ($r=0.79$, $p=0.001$) indicated that trials underestimating population size also underestimated the standard error resulting in a low coefficient of variation, particularly for $k=3$ (Fig. 2). This creates the impression that the estimate is more accurate than it actually is, while trials yielding an overestimate of the

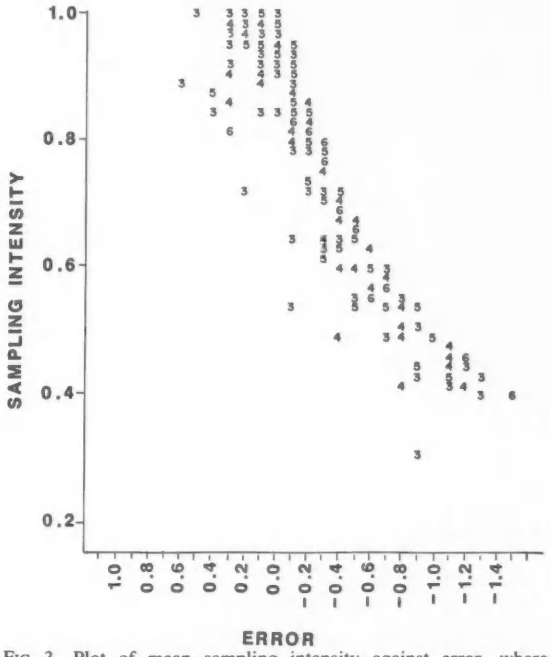

FIG. 3. Plot of mean sampling intensity against error, where error $=(N-\hat{N})\cdot N^{-1}$. Numbers plotted on the graph represent values for number of searches (k).

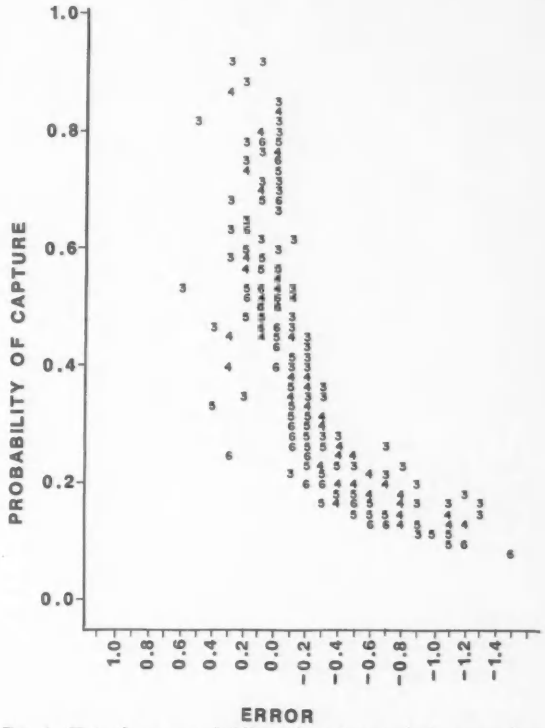

FIG. 4. Plot of mean probability of capture against error, where error $=(N-\hat{N})\cdot N^{-1}$. Numbers plotted on the graph represent values for number of searches (k).

population size also resulted in an inflated coefficient of variation leaving the impression that the estimate is less accurate. The number of trials resulting in an overestimate declined as sampling intensity increased. Estimates lying within 10% of the true population size were obtained with a sampling intensity of $\geq$70%. However at high sampling intensities, large underestimates were still observed in some simulations especially for $k=3$ (Fig. 3). The accuracy of the estimates also improved as the probability of detecting a seal hole increased especially above a probability of detection $\geq$0.3 (Fig. 4). However, at high probabilities of detection a large number of underestimates were still obtained, when $k=3$.

We examined sampling intensity, coefficient of variation and probability of capture together to determine if estimates with accurate estimates could be obtained. Applying the restriction of a sampling intensity of $\geq$0.5, coefficient of variation of $\leq$0.9 and probability of capture $\geq$0.1, 94% of 1044 simulations meeting these criteria had estimates lying within $\pm$25% of the true population size. This proportion increased to 95% if samples with $k=3$ were ignored. Conversely only 14% of the simulations not meeting these criteria were within $\pm$25% of the correct population size. Estimates within $\pm$10% of the true population size were obtained in 92% of 849 trials satisfying the criteria of a sampling intensity of $\geq$0.85, probability of detecting a seal hole $\geq$0.35 and a coefficient of variation $\leq$0.3. This proportion increased to 95% if simulations with $k=3$ were excluded. Among simulations not meeting the restriction criterion, 21% of 350 trials differed from the true population size by $\leq$10%. Similar results could also be obtained by reducing the coefficient of variation, but this approach resulted in an increase in the number of accurate estimates incorrectly identified as differing from the true population by >10%.

Field Surveys

It was not possible to assess the effective detection distance of the dogs. Normally the dogs ran to seal structures <500 m from the transect they were searching, but on occasion they have detected ringed seal lairs from a distance of 1.6 km. An examination of the survey results from Barrow Strait shows that a large proportion of the total number of seal holes found in study plots remain undetected even after three surveys and that this proportion varied between plots. In plots surveyed six times only 61 to 81% of the holes were located in the first three searches (Table 1).

The removal model was applied to survey results from Barrow Strait (Table 2). No estimate of number of seal holes was obtained for plot 849 because the survey data did not satisfy the failure criterion given by equation (3). When this plot was surveyed air temperatures were close to 0°C. We believe the dogs were not able to survey this plot effectively in the allotted time because they constantly broke through the surface layer of snow making travel over the snow quite difficult.

All chi-square values were nonsignificant. However, applying the criteria developed above, it is likely that all estimates from the removal model lie within 25% of the true population size with the exception of plots 843 and 846 (Table 2). Estimates with a bias of less than 10% appear to have been obtained in only two of nine plots in 1984, seven of nine plots in 1985 and 12 of 14 plots surveyed in 1986 (Table 2).

The quality of the survey results improved from 1984 to 1986. Mean coefficient of variation declined from 0.69 in 1984 to 0.22 in 1985 to 0.16 in 1986; mean sampling intensity increased

TABLE 1. Proportion of holes found during individual surveys of plots searched three, four, five, and six times.

Year	Number of plots searched	Mean total number of seal holes per plot	Proportion of holes located (%)					
			First search	Second search	Third search	Fourth search	Fifth search	Sixth search
			3 Searches					
1984	2	17	50	26	24			
1985	1	4	100	0	0			
1986	—							
			4 Searches					
1984	2	17	35	24	24	18		
1985	—	—	—	—	—	—		
1986	9	18	61	21	12	6		
			5 Searches					
1984	3	21	27	16	17	16	25	
1985	4	18	40	23	23	5	8	
1986	3	12	42	33	8	17	0	
			6 Searches					
1984	2	21	36	17	10	24	5	
1985	3	18	42	21	19	9	2	
1986	2	17	41	15	12	18	6	

from 0.70 in 1984, to 0.92 in 1985, and to 0.94 in 1986. The mean probability of detecting a seal hole increased from 0.29 in 1984, to 0.44 in 1985, and to 0.52 in 1986. Looking only at changes in probability of detecting a seal hole the improvement in results could be attributed to an increase in survey effort from 1984 to 1986, the use of only one dog during the surveys in 1985 and 1986 ($F = 7.6$, df = 1,32 $p < 0.001$) and a reduction in plot size in 1986 from 4.0 to 2.25 km^2 ($F = 4.4$, df = 1,32, $p < 0.05$).

Rough ice and pressure ridging interfered with the dog's ability to detect seal holes ($r = -0.61$, $p = 0.0002$, $N = 32$), but windspeed, temperature, and snow depth did not have any affect.

Densities of seal holes did not differ significantly between years. The highest densities were observed in 1986 ($x = 7.9$ holes·km^{-2}, SE = 1.0, $N = 14$), followed by 5.5 holes·km^{-2} (SE = 0.9, $N = 9$) in 1984 and 4.8 holes·km^{-2} (SE = 0.7, $N = 9$) in 1985. Because the estimates from plots 843 and 846 in 1984 were considered to be severely biased, and no solution to equation (1) was obtained for the survey results from 849 we have used the actual number of holes located in these plots which likely results in an underestimate of the true density for this year.

Hole to seal ratios were obtained for five female and three male seals from the following plots; one in plots 847 and 859, and two in plots 854, 853, and 862. The two animals caught in plot 862 were immature females. Each maintained three holes. The adults maintained an average of 3.5 holes per seal (SE = 0.2). The average seal to hole ratio for all animals combined was 3.4 (SE = 0.2).

Seal densities were calculated by dividing hole densities by 3.4. Densities were 2.3 seals·km^{-2} in 1986, 1.4 seals·km^{-2} in 1985, and 1.6 seals·km^{-2} in 1984.

Discussion

The removal model was developed for enumerating large populations, where a major proportion of the animals can be permanently removed. This technique is considered to be less efficient than mark–recapture methods (Seber 1982; Skalski and Robson 1982). Unfortunately the dogs show little interest in returning to previously discovered holes, making it unlikely that the assumption of equal detection of marked and unmarked holes would be satisfied.

Below populations of 200 animals Zippin (1956) warns that his formulae underestimate the standard error and that two standard errors on each side of the estimate represent 90% confidence limits and not 95% limits. In our simulations we purposely selected small populations of 10 to 40 seal holes to reflect conditions we expected to encounter in the fast ice breeding habitat. This approach showed that the standard error was not a valid statistic by itself to assess the quality of the population estimate. Similarly the chi-square test was not effective in detecting departures from the assumption of equal probability of capture. However, estimates lying within 10% of the true population size may still be obtained using the removal method provided the plot is searched ≥ 4 times, sampling intensity is ≥ 0.85, the coefficient of variation is ≤ 0.3 and the probability of detecting a seal hole is ≥ 0.35.

The use of one dog per plot and a reduction in plot size significantly improved survey results. The smaller plot size permitted the dog to make more frequent traverses of the plot during the allocated search time, which would ensure that the assumptions that all seal holes have an equal probability of detection and the detection of seal holes is independent are satisfied. Plot size should be selected so that the majority of plots will contain at least one seal (Greig-Smith 1964), which suggests a minimum plot size of 0.6 km^2 for the areas surveyed in this study. A reduction in plot size would also permit an increase in the number of plots that can be surveyed within a season.

The findings that windspeed and air temperature had no effect on the dog's ability to detect seal holes were unexpected. They likely result from the fact that surveys were only conducted under conditions favourable to the dog's handlers. Surface topography did affect the dog's ability to detect seal holes. We believe that plots with considerable rough ice and pressure ridg-

TABLE 2. Summary of survey results from study plots surveyed during March to May, 1984–86 in Barrow Strait NWT. The survey plots had an area of 4 km^2 in 1984 and 1985 and 2.25 km^2 in 1986. Two dogs were used in the 1984 surveys. Only one dog was used in 1985 and 1986. Estimates likely to differ from the true population size by >10% are denoted by ‡ and >25% by *.

Plot	K	Total holes found	Estimated population	Coefficient of variation	Proportion of population detected	Probability of detecting a seal hole
				1984		
841	5	6	6	0.04	0.97	0.50
842	5	22	30	0.50	0.72	0.23‡
843	4	14	38	1.63	0.37	0.11*
844	4	20	29	0.75	0.68	0.25‡
845	6	29	52	0.83	0.56	0.13‡
846	3	13	26	1.35	0.50	0.21*
847	6	13	13	0.03	0.98	0.49
848	3	21	26	0.41	0.79	0.41‡
849	5	36	—	—	—	—
				1985		
851	3	4	4	0.0	1.0	1.0
852	5	14	17	0.63	0.81	0.29‡
853	5	21	23	0.18	0.90	0.37
854	6	15	16	0.16	0.95	0.40
855	6	17	17	0.04	0.98	0.49
856	6	21	26	0.32	0.82	0.25
857	5	12	13	0.44	0.92	0.40‡
858	5	26	29	0.17	0.89	0.36
859	8	26	27	0.05	0.97	0.40
				1986		
861	6	12	13	0.23	0.95	0.39
862	5	14	14	0.10	0.97	0.49
863	5	10	10	0.12	0.96	0.47
864	4	8	8	0.02	0.98	0.64
865	6	22	28	0.35	0.79	0.23‡
866	4	20	22	0.21	0.90	0.43
867	4	27	31	0.20	0.86	0.39
868	5	12	14	0.78	0.86	0.33‡
869	4	19	19	0.01	0.99	0.72
8610	4	29	30	0.08	0.96	0.55
8611	4	18	18	0.02	0.99	0.67
8612	4	23	25	0.13	0.94	0.50
8613	4	12	12	0.00	1.0	0.80
8616	6	6	6	0.00	1.0	0.74

ing were more difficult for the dog to traverse, reducing its ability to effectively survey the plot. Plots with extensive rough ice and pressure ridging may also create local conditions of high turbulence, making it more difficult for the dog to track a scent.

Hole to seal ratios have been estimated for ringed seals using ratio tagging (2–4 holes per seal; Burns and Kelly 1982; Kelly 1985), and behavioural methods (1–4 holes per seal; Finley 1979). Unfortunately all methods are subject to logistical problems, consequently sample sizes are small. Our method of removing seals is time consuming and limited in the number of animals that can be captured. It assumed that we have located all holes used by the animal removed, no holes are shared with other animals on a regular basis and our activities on the ice have not resulted in disturbed animals abandoning the study area. Presently, it is not possible to test these assumptions. However, our estimate does lie within the range outlined above and is similar to an estimate of 3.8 holes per seal, we derived for ringed seals during a behaviour study on Baffin Island after correcting for the fraction of the population (80%) hauled out

TABLE 3. Comparisons between seal density (seals/km^2) obtained from dog surveys and estimates obtained from aerial surveys of hauled out animals. Standard errors are in parentheses. Seal densities from the present study were obtained by dividing the density of seal holes by 3.4.

This Study	Aerial Surveys		
Density	Year	Density	Source
2.35 (0.29)	1986	1.17 (0.05)	M. Kingsley, unpubl. data[a]
1.43 (0.19)	1985	1.07 (0.05)	Barrow Strait transects
1.64 (0.28)	1984	1.07 (0.05)	lying between 95°W and 98°W
	1982	0.90 (0.08)	Kingsley et al. 1985.
	1981	1.16 (0.21)	Stratum 6
	1980	0.85 (0.09)	
	1975	0.69 —	Smith et al. 1978
	1975	0.82 —	Finley (1976) average from Smith et al. 1978

[a]M. C. S. Kingsley, Freshwater Institute, Dept. Fisheries and Oceans, Winnipeg, Manitoba, R3T 2N6.

on the ice at one time (Smith and Hammill 1981). Applying a ratio of 3.4 holes per seal to estimates of seal hole density shows that densities may be 1.3 to 1.9 times higher than estimates obtained from aerial surveys (Table 3). These estimates do not take into account pup production or immature animals who appear to be excluded from the breeding habitat (McLaren 1958; Smith and Hammill 1981; Hammill and Smith 1989). In this study the proportion of birth lairs varied between 20 and 40% (Hammill and Smith 1989). Successful predation by polar bears was observed at 5 to 26% of the birth lairs located by the dog with pups forming 75 to 100% of the catch (M. O. Hammill, unpubl. data). Such variation between years indicates that major changes had occurred in productivity and composition of the population in the fast ice even though significant differences in densities were not observed.

Aerial surveys of ringed seals are able to cover large areas quickly and relatively inexpensively. Current techniques are well developed (coefficient of variation <20%; Kingsley et al. 1985). However, further advances are not possible until corrections for plot composition and animals not hauled-out on the ice can be made. This information is presently only available from dog surveys. Unfortunately this technique is not suited to surveying large areas. One solution to the problem of monitoring ringed seal populations may be to coordinate the dog search and aerial survey techniques, where point estimates from the ground searches could be used to correct estimates from aerial counts.

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Changes in Species Interactions of the Lake Superior Fisheries System After the Control of Sea Lamprey as Indicated by Time Series Models[1]

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Stone, J. N., and Y. Cohen. 1990. Changes in species interactions of the Lake Superior Fisheries System after the control of sea lamprey as indicated by time series models. Can. J. Fish. Aquat. Sci. 47: 251–261.

Interspecific and intraspecific interactions of fish species in the Canadian commercial fisheries changed following the control of sea lamprey (*Petromyzon marinus*). These changes were detected by a multivariate time series (MVTS) analysis of monthly time series of catch-per-unit-effort for lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), lake herring (*C. artedii*), chubs (*Coregonus* spp.), walleye (*Stizostedion vitreum*), and yellow perch (*Perca flavescens*). The identified MVTS models reflected known trophic relationships among fish species and indicated that significant intraspecific interactions were more numerous than interspecific interactions. Lake trout interactions with other species appear to have changed due to stocking and diet change. Single species time series models confirmed the lag structure of the MVTS models and were useful for forecasting abundance.

Les interactions interspécifiques et intraspécifiques des espèces de poissons des pêches commerciales canadiennes ont varié à la suite du contrôle de la grande lamproie marine (*Petromyzon marinus*). Ces changements ont été observés par une analyse multivariés des séries chronologiques mensuelles des prises par unité d'effort du touladi (*Salvelinus namaycush*), du grand corégone (*Coregonus clupeaformis*), du cisco de lac (*C. artedii*), des *Coregonus spp.*, du doré (*Stizostedion vitreum*) et de la perchaude (*Perca flavescens*). Les modèles déterminés par les séries chronologiques multivariées reflétaient les liens trophiques connus entre les espèces de poissons et indiquaient que les interactions intraspécifiques importantes étaient plus nombreuses que les interactions interspécifiques. Les interactions entre les touladis et les autres espèces semblent avoir changé à cause de variations dans l'empoissonnement et le régime alimentaire. L'utilisation de modèles déterminés par des séries chronologiques pour une seule espèce a permis de confirmer les lacunes des modèles pour plusieurs espèces et a permis de prédire l'abondance.

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The invasion by sea lamprey (*Petromyzon marinus*) and the subsequent efforts to eradicate it were major perturbations to the fish community of Lake Superior. Following a large perturbation, structural changes in the fish community — as measured by species interactions — should occur. Species interactions are by our definition, measured by parameter matrices which are identified through multivariate time series (MVTS) analysis. Knowledge of these structural changes can improve understanding of the fish community and its management.

Sea lamprey were first reported in Lake Superior as early as 1938 and by 1949 individuals were observed at both the eastern and western ends of the lake (Smith and Tibbles 1980). Sea lamprey are anadromous in the Atlantic Ocean. In the Great Lakes they spawn in streams, where the larval stage remains sedentary and filter feeds for up to 7 yr (Hardisty and Potter 1971). Following transformation, they migrate downstream into the Great Lakes where they live for 12 to 18 mo before migrating back to streams to spawn and die. During the adult phase, sea lamprey are parasitic; they feed by attaching themselves to fish and consuming body fluids and blood (Lennon 1954). The attacks may or may not end with the death of the parasitized fish.

The effort to eradicate sea lamprey in Lake Superior began by placing barriers and weirs in streams below potential spawning areas. From 1953 to 1960 about 55 barriers were placed for varying lengths of time in Lake Superior tributaries (Smith and Tibbles 1980). The effectiveness of the barriers in controlling sea lamprey abundance was uncertain as its numbers in Lake Superior increased (Lawrie 1970). In 1956, a lampricide, 3-trifluoromethyl-4-nitrophenol, was found to have toxic effects on larval lampreys with little harm to other fishes (Applegate and King 1962; Applegate et al. 1961). Chemical treatment began in Lake Superior tributaries in 1958 when 12 streams were treated (Smith et al. 1974). Yet, because treatment was directed at the larval stage, a significant decrease in adult spawning-phase lampreys was not observed until 1962, when an 86% decline from 1961 occurred. With continued control by lampricide, the average sea lamprey population for 1973–78

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was reduced to 8% of its 1958–61 average (Smith and Tibbles 1980).

The effects of sea lamprey on the native fish species in Lake Superior were most evident in the commercial catch of lake trout (*Salvelinus namaycush*), which decreased from 2 131 000 kg in 1950 to 224 000 kg in 1960 (Baldwin et al. 1979; table 106). Sea lamprey induced scars also appeared on lake whitefish (*Coregonus clupeaformis*), catostomids (*Catostomus* spp. and *Moxostoma* spp.), and walleye (*Stizostedion vitreum*) (Smith and Tibbles 1980). With the reduction in the population density of large predatory fishes (e.g. lake trout), an initial increase in the abundance of some prey species (e.g. *Coregonus hoyi*) occurred (Christie 1974). However, with the decrease in the abundance of large fish species, the commercial fisheries targeted the smaller, less utilized fish species such as chubs (*C. nigripinnis*, *C. zenithicus*, *C. kiyi*, *C. reighardi*, and *C. hoyi*) (Lawrie and Rahrer 1973). In addition to the changes imposed by sea lamprey species composition in Lake Superior was altered by stocking of exotic fish species such as Pacific salmonids (Emery 1985). Furthermore, rainbow smelt (*Osmerus mordax*), a nonindigenous species, became abundant and replaced lake herring as the major food source of lake trout (Dryer et al. 1965). Following the control of sea lamprey, the lake trout fishery was managed through quotas and stocking (MacCallum and Selgeby 1987). Despite these efforts, the commercial yield of lake trout in Lake Superior did not return to its level prior to the invasion by sea lamprey.

Multivariate time series models have been used to analyze the community structure of fish and to forecast fish population abundance (Cohen and Stone 1987; Mendelssohn and Cury 1987). This inductive approach utilizes long sequences of time-related data to identify a model in terms of interactions and time lags between and within individual time series (e.g. of fish species abundance indices). To understand changes in the fish community in Lake Superior during 1948 to 1976, we identified, fitted, and validated MVTS models to the catch and effort data of the Canadian commercial fisheries for the period prior to effective sea lamprey control (1948–61) and the period of effective control (1962–76). The purpose of the analysis was to determine (1) what, if any, structural changes have occurred in the fishery, and (2) if the structure identified could be used for forecasting fish abundance. By our definition, the structure of the fish community is identified by the significant elements of the lag matrices of the MVTS models (see below). The analysis revealed feedback relationships among various species, corroborating some known biological facts about the system but also reflecting other unexplained interactions. Changes in the community structure between the prelampricide period and the lampricide period occurred. The models, though useful for forecastingundance and revealing community structure, have limitations which we discuss.

Data

All commercial fishermen in Ontario have been required to complete a daily report of their catch since 1948 (Hile 1962). The report includes date, location, species caught, weight by species, gear type, and effort. Each species caught, by date, constituted an individual record in the data set, which in turn was organized into seven statistical districts (Smith et al. 1961) or more recently into 34 management zones (MacCallum 1983). We obtained the data from the Fisheries Branch, Ontario Ministry of Natural Resources, Toronto and Thunder Bay, Ontario.

We summarized the data by month for the yield and effort of the gill net fishery. Gill nets had yielded the largest catch and had been used consistently during 1948–76. However, in 1949–52 the twine used to make gill nets was changed from cotton to nylon in the United States fisheries of Lake Superior, resulting in a 2.25-fold increase in efficiency for the harvest of legal-sized lake trout (Pycha 1962). Additionally, nylon was found to be 4.3 times more effective in capturing lake herring than cotton and 2.2 times for chubs (Dryer and Beil 1964). The time at which a change from cotton to nylon for the Canadian fisheries occurred is unknown, as is the amount of change in catch efficiency related to this switch. We did not apply correction factors to the data to account for increased catch efficiency. Thus, our results and analysis are more conservative than those which we might have obtained had we used correction factors for changes in catch efficiency.

Methods

Multivariate time series models were used to investigate differences in the structure of the fisheries system between the prelampricide period (1948–58) and the lampricide period (1963–73). System structures were deduced from the significant interactions among species abundances of models identified by the methods described below. Time series of catch-per-unit-effort (CPUE) were modelled. To validate the models, model fit and model-based forecasts of CPUE were compared by three statistics to the actual data and to fits and forecasts from two other models: (1) CPUE one year prior to the forecasted period, and (2) univariate autoregressive time series models. The three statistics and the models are described below.

Multivariate Time Series Analysis

Model identification, fitting, and verification followed the procedures outlined by Box and Jenkins (1976) and Tiao and Box (1981); see Cohen and Stone (1987) for an example. The software (SCA) is described by Liu et al. (1983). Generally, MVTS models are described by the equation

$$(1)\quad \phi_p(B^n)z_t = \theta_q(B^m)a_t,$$

where ϕ is a polynomial matrix of degree p of autoregressive (AR) parameters (i.e. $\phi_p B^n = I + \phi_1 B^1 + \phi_2 B^2 + \ldots$), B^n is a n-order backshift operator e.g. $B^2 z_t = z_{t-2}$), z_t is a vector of dimension k of the (possibly transformed) time series x_t at time t, θ is a polynomial matrix of degree q for the moving-average (MA) parameters, and a_t is a vector of k time series which have multivariate normal distributions with mean zero and a constant covariance matrix over time (i.e. this matrix included the statistical error called white noise). An AR process is weighted on the data (i.e. $x_t = b_1 x_t + \ldots + b_p x_{t-p} + e_t$) whereas a MA process is weighted on the white noise (i.e. $x_t = b_0 e_t + b_1 e_{t-1} + \ldots + b_q e_{t-q}$); e_t is a random process with mean zero and variance s_e^2.

As a specific example of model (1), consider six interrelated time series and assume that the value of each time series at time t depends on all time series of time $t-1$ and $t-12$. Furthermore, assume that to improve the fit (in terms of reducing the residuals to "white noise"), a MA term based on lag 1 needs to be applied to the fit of model. Then equation (1) becomes

$$(2)\quad (I - \phi_1 B - \phi_{12} B^{12})\, z_t = (I - \theta_1 B)\, a_t;$$

where I is the identity matrix z_t is a vector of six stationary (constant mean and variance) time series, and the vector a_t contains six time series of white noise.

Model Fit and Forecast Comparisons

In the process of identifying a MVTS model, the data are fit such that the residuals are reduced to white noise as best as possible (Tiao and Box 1981; Liu et al. 1983). To understand how the model fits the data and to allow comparison among different models, three statistics were derived from comparisons between the data and model fits, and the data and model-based forecasts: Pearson correlated coefficient, mean absolute percentage error (MA%E), and mean percentage error (M%E). The MA%E was calculated by

$$(3)\quad \text{MA\%E} = \frac{1}{(T_2 - T_1 + 1)} \sum_{t=T_1}^{T_2} |(O_t - P_t)/O_t|,$$

(Roff 1983; Armstrong 1985, p. 346–362) where T_1 and T_2 are the initial and the final values in the time series, O_t are observed CPUE, and P_t are fitted or forecasted CPUE in year t. Fitted CPUE correspond to the period in which the observed data were used for parameter identification; whereas the observed data for the period of the forecast CPUE were not used in parameter estimation. The M%E was calculated as in equation (3) with the absolute value removed. M%E, therefore complements MA%E by indicating whether, on the average, the fits (or forecasts) were greater or less than the observed values. The Pearson correlation coefficient indicates how closely related are the trends between two data sets. The MA%E and M%E statistics reflect the closeness of the data to the fits (or forecasts). For example, if the predictions were exactly x units above the data then the correlation would be 1.0 but MA%E and M%E would depend on the values of the data and x. We used the above statistics to compare data to model fits and forecasts of 6,12, and 24 mo, and, where feasible, 48 and 60 mo. Standard deviations for MA%E were calculated by the bootstrap method using a replication of 1000 (Efron 1982). The bootstrap is a nonparametric estimation procedure for measures of error (e.g. standard deviation) drawn from subsampling the original data.

Comparisons of Models

To investigate the goodness of fit of the MVTS models relative to other models, two univariate autoregressive models were identified. These models were simpler (i.e. only one time series) and easier (i.e. fewer decisions need to be made by the user for the model identification) than the MVTS models. The first, the lag 12 model, included only a lag of 12 mo i.e.

$$(4)\quad z_t = z_{t-12} + a_t,$$

where z_t is the stationary time series value at time t and a_t is a white noise series value at time t. The underlying assumption was that an estimate for the present month's CPUE is the CPUE in the same month one year ago. The second, the FORECAST model, was

$$(5)\quad \phi_p(B^n)\, z_t = a_t,$$

where z_t and a_t are as in equation (4), B^n is a backward shift operator (equation (1)), and $\phi_p(\cdot)$ is a polynomial of degree p with vector coefficients for AR parameters (i.e. species interactions and moving average terms are not included). We used the SAS (1984) procedure FORECAST to identify and estimate the parameters of model (5). The procedure, after removing a constant trend, regresses the residuals against the lag in a Yule-Walker framework. Lags are included if they contribute significantly ($p<0.05$) in a stepwise regression procedure.

The fits and forecasts of the lag 12 (equation (4)) and the FORECAST (equation (5)) models were compared with the MVTS model (equation (1)) using the three statistics described above (Pearson correlation, MA%E, and M%E). A better fit (e.g. in terms of correlation and residual analysis) of one model compared with another may indicate a more appropriate model, but also may be the outcome of overfitting. Thus, to further validate the models and address the problem of overfitting, forecasts were evaluated, which compare data not included in the parameter identification and estimation process of model building.

Species Interactions

To investigate changes in system structure between the period prior to effective sea lamprey control (1948–61) and the period of effective control (1962–76), we identified MVTS models of the CPUE of six fish species for four periods of 140 mo (11 2/3 yr) each starting with January of 1948, 1953, 1958, and 1963. A length of 140 mo was chosen to (1) use sufficient data for parameter estimation and (2) allow a minimum of 28 mo for forecasting of CPUE (i.e. model validation) after the period starting in 1963. Because a 140-mo period starting in January ends in August, comparisons of forecasts for three fall seasons (when fish yield was traditionally the highest) for the period starting in 1963 were possible.

The data starting in 1948 and 1963 do not overlap and correspond respectively to the time prior to and during effective sea lamprey control. We refer to these two periods as the prelampricide and the lampricide periods. The two intermediate time periods, starting in 1953 and 1958, are called Intermediate I and Intermediate II, respectively. These intermediate periods were used to investigate changes in model structure (i.e. changes in the parameters of the AR and MA matrices) as the effect of sea lamprey control was taking place.

Nonstationarity and seasonal trends were first removed from the data. To stabilize the variance, all time series were transformed with $y_{it} = \sqrt{1 + x_{it}}$ where x_{it} is the CPUE at time t for species i. Fisheries in Lake Superior are also highly seasonal and the series are not stationary. Therefore, all data were differenced according to $z_t = y_t - y_{t-12}$ where z and y are vectors of dimension six.

To determine the extent of interspecific interactions and to relate model structure to what is known about the Lake Superior fishery, we used CPUE. When applied on an annual basis (e.g. December 1948, December 1949, . . ., December 1976) CPUE reflects the abundance of a species (Gulland 1964; Peterman and Steer 1981; Bannerot and Austin 1983). CPUE at different times of the year also reflects the catchability of fish and therefore life history and distributional characteristics. For example, lake herring aggregate to spawn over shoals in late fall, at which time CPUE is high. They disperse in the lake during the summer, resulting in low CPUE. The relative change of the CPUE within a season can be used to improve forecasts. However, the monthly samples do not give independent observations on the recruitment of year classes and may result in problems due to oversampling the dynamics of interest (see Chelton (1983) and Welch (1987)). We assumed that the data indirectly reflect the fisheries system as a whole, including inputs such as fishers'

TABLE 1. Significant ($p \leq 0.05$) parameter estimates of the model $(I-B^{12})\ (I-\phi_1 B^1-\phi_{12}B^{12})\ (I-\phi_{24}B^{24})\ x_t=a_t$ identified for the prelampricide period. Nonsignificant parameters were set to zero and appear as blanks in table. Columns lead rows (i.e. species in row is influenced by species in column). The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chub spp.; WL, walleye; YP, yellow perch.

	LT	WF	LH	CH	WL	YP
ϕ_1						
LT		−0.24		−0.05		
WF	−0.11	0.42	0.03			
LH						
CH						
WL					0.31	
YP						
ϕ_{12}						
LT	−0.74	−0.56				
WF		−0.36		−0.04		
LH	−1.54		−0.46			
CH				−0.58		
WL						
YP						−0.54
ϕ_{24}						
LT	−0.35	−0.24				0.09
WF		−0.35		−0.04		
LH	−2.40					−0.55
CH				−0.40		
WL					−0.33	
YP						−0.46

TABLE 2. Significant ($p \leq 0.05$) parameter estimates of the model $(I-B^{12})(I-\phi_1 B^1-\phi_{12}B^{12})\ (I-\phi_{24}B^{24})x_t=a_t$ identified for the intermediate *I* period. Nonsignificant parameters were set to zero and appear as blanks in table. Columns lead rows (i.e. species in row is influenced by species in column). The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chub spp.; WL, walleye; YP, yellow perch.

	LT	WF	LH	CH	WL	YP
ϕ_1						
LT	0.20	0.39				
WF		0.36	0.05			
LH				−0.49		
CH				0.33		
WL				0.16	0.33	−0.17
YP						
ϕ_{12}						
LT	−0.50					
WF		−0.24		−0.05	−0.15	
LH				−0.64		
CH				−0.34	0.51	
WL					−0.28	
YP					0.58	−0.59
ϕ_{24}						
LT	−0.50	0.24	−0.07			
WF		−0.55		−0.05		
LH				−0.40	0.57	
CH	−0.42	0.76		−0.22		−0.18
WL			−0.10			
YP		0.99			0.33	−0.39

TABLE 3. Significant ($p \leq 0.05$) parameter estimates of the model $(I-B^{12})(I-\phi_1 B^1-\phi_{12}B^{12})\ (I-\phi_{24}B^{24})x_t=a_t$ identified for the intermediate II period. Nonsignificant parameters were set to zero and appear as blanks in table. Columns lead rows (i.e. species in row is influenced by species in column). The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chub spp.; WL, walleye; YP, yellow perch.

	LT	WF	LH	CH	WL	YP
ϕ_1						
LT						
WF						
LH						
CH		−0.33		0.39		
WL	0.46				0.27	
YP				0.26		0.14
ϕ_{12}						
LT	−0.49					
WF		−0.65		−0.12	0.08	
LH			−0.42			
CH				−0.51		
WL	−0.49				−0.57	
YP			0.09			−0.71
ϕ_{24}						
LT					0.11	0.08
WF		−0.46				
LH			−0.27			
CH				−0.46		
WL					−0.73	
YP						−0.42

behavior, market prices, regulations, and life history of the fish species. Our subsequent analysis should be interpreted with this perspective in mind.

CPUE was calculated by dividing the total monthly yield (in kilograms) by the total length of gill net (in kilometres) used in the month. The six species or species groups used in the analysis were lake trout, lake herring, lake whitefish, chubs, walleye, and yellow perch: the first four have been the major commercial species in Lake Superior; the last two species were consistently caught during 1963 to 1976.

Results and Discussion

The structure of the fisheries system has changed from the prelampricide to the lampricide period: the number of interspecific interactions (as indicated by the number of significant parameters in the matrix ϕ of the MVTS models; Tables 1–4), decreased from the prelampricide to the lampricide period for lake trout and lake whitefish; however, they increased for lake herring, walleye, chubs, and yellow perch. The goodness of fit (as measured by correlation and MA%E) of the models differed between the prelampricide and the lampricide periods with the direction of change varying among the species and fit statistics. In the following sections, where we describe the results in further detail, models refer to the MVTS models unless otherwise stated.

MVTS Models

Autoregressive (rather than moving average) parameters governed the models identified for the four time periods (Tables 1–4). Lags of 1, 12, and 24 mo were present in all models.

TABLE 4. Significant ($p \leq 0.05$) parameter estimates of the model $(I - B^{12})(I - \phi_1 B^4 - \phi_4 B^1 - \phi_{12} B^{12})\ (I - \phi_{24} B^{24}) x_t = a_t$ identified for the lampricide period. Nonsignificant parameters were set to zero and appear as blanks in table. Columns lead rows (i.e. species in row is influenced by species in column). The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chub spp.; WL, walleye; YP, yellow perch.

	LT	WF	LH	CH	WL	YP
ϕ_1						
LT	0.34					
WF			−0.19			
LH						0.48
CH				0.43	0.34	
WL				−0.13	0.26	0.21
YP						0.46
ϕ_4						
LT						
WF						
LH				−0.15		
CH				0.20		
WL	1.74		−0.30	−0.13		
YP						0.17
ϕ_{12}						
LT	−0.38					
WF		−0.51		−0.21		
LH			−0.28			
CH	0.77			0.19		0.29
WL					−0.29	
YP				−0.44		−0.42
ϕ_{24}						
LT						
WF		−0.43				
LH			−0.23			0.35
CH			0.15			
WL					−0.25	
YP	0.83					
θ_1						
LT						
WF		−0.30	−0.25			
LH						0.49
CH					0.44	
WL						
YP						

Only in the lampricide period model was the lag at 4 mo present. Furthermore, a MA term of 1 mo was included in this model. The presence of lags of 1, 4, 12, and 24 mo only in the identified models does not indicate that other lags were unimportant for individual species. Information about the interactions at lags longer than 24 mo may be encapsulated in the model (although the time series may not be of sufficient length to identify longer lags). The models do, however, result in the most parsimonious models.

For most species, its past abundance was more influential than the past abundance of other species in forecasting that species' abundance, as shown by intraspecific, as opposed to interspecific interactions (i.e. significant parameters on the diagonal versus the off diagonal of the matrices ϕ; Tables 1–4), dominating in the models. Of all possible intraspecific interactions 65% were significant while 14% of the interspecific interactions were significant for the lags identified (Tables 1–4). Single species time series models, therefore, may be as useful as MVTS models for forecasting a species' CPUE (see below). Furthermore, 81% of the possible intraspecific interactions were significant at the yearly lags (e.g. 12 and 24 mo) as opposed to 44% at other lags. This difference reflected the importance of distributional characteristics of fish in determining the CPUE for a particular month (e.g. higher CPUE when fish are aggregated for spawning versus lower CPUE when fish are dispersed).

To facilitate interpretation of species interactions (i.e. community structure) — as reflected by the identified models — we expanded the model equations (shown in the captions of Tables 1–4) and lumped lags into four classes; within-season (0–6 mo), 1-yr (7–18 mo), 2-yr (19–30 mo), and 3-yr (31–42 mo). Additionally, all four lag-classes were combined to provide an overview of species interactions. These five classes are shown separately in Figs. 1 and 2 (a)–(e). The arrows in the figures reflect the interactions with lags. For example, the arrow with the negative sign between the boxes representing lake trout and lake herring in Fig. 1e indicates that when the CPUE of lake trout was high, the CPUE of lake herring was low 3 yr later (an expected result for a predator–prey relationship). Furthermore, as indicated by the arrow with a positive sign from walleye to itself (Fig. 1b), when the CPUE of walleye was high, its CPUE was high within the same season (i.e. 1 mo later).

The number of significant species interactions during the prelampricide period increased from 34 (Fig. 1) to 41 during the postlampricide period (Fig. 2). During the Intermediate II period (starting in 1958), the number of significant parameters (28) was the least. This was the only period which spanned the prelampricide and lampricide periods. Because the system was in transition from ineffective to effective sea lamprey control, and because the lags between pairs of species were most likely changing, significant interactions were, presumably, less easily identified by a single constant parameter. The number of interspecific interactions between the prelampricide period and the lampricide period decreased for lake trout and lake whitefish but increased for lake herring, chubs, walleye, and yellow perch (Figs. 1 and 2). Note that significant parameter values in the AR matrices reflect, by our definition, species interactions; however, these interactions may not necessarily be direct predation or competition. Reasons for the changes in significant parameter values are suggested next.

Lake Trout

Major changes in the management of lake trout occurred between the prelampricide and the lampricide periods: in the former, total commerical harvest was unrestricted; in the latter, quotas large enough only to provide biological information were imposed (Pycha and King 1975). With an effective sea lamprey control program implemented, large scale stocking of yearling lake trout began throughout the lake. In the Canadian waters, an annual average of 484 000 age I and older fish were planted between 1958 and 1975. Subsequently, over 90% of the inshore harvest of lake trout was from hatchery fish during 1966–70 (Lawrie and MacCallum 1980). Such stocking undoubtedly affected the system structure as reflected in Figs. 1 and 2: prior to stocking (Fig. 1), lake trout abundance (as measured by CPUE) affected and was affected by other species (as expected for a predatory fish); during stocking (Fig. 2), lake trout abundance affected other species, but was not affected by the abundance of other species.

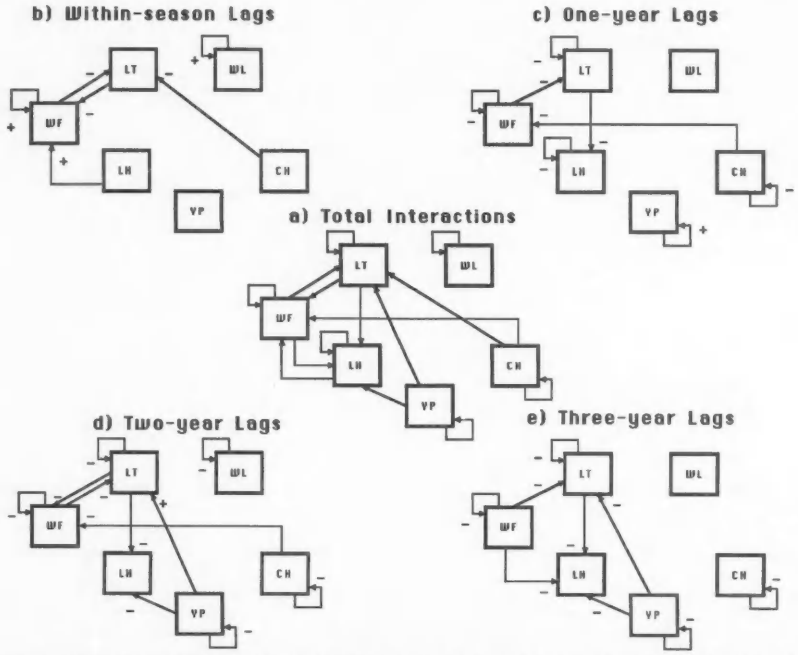

FIG. 1. Simplified web of interactions of CPUE of six commercial fish species in Lake Superior for the prelampricide period according to the identified MVTS model (see the equation in the caption of Table 1). The CPUE for the species at the tail of the arrows are leading (i.e. "influencing" the CPUE) for the species at the head of the arrows; + indicate positive interactions (i.e. high CPUE forecasts high CPUE); − indicate negative interactions. The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chubs; WL, walleye, YP, yellow perch.

Prey abundance may have influenced the abundance of adult lake trout by at least two means: (1) changes in the food base for adult lake trout; and (2) changes in competition with (or predation on) young lake trout. Since harvested lake trout in the lampricide period are largely stocked, no interactions with young (less than age I) lake trout are possible; thus, interspecific interactions during the lampricide period should reflect factors influencing the adults. The two-way interactions between lake trout and other species during the prelampricide/prestocking period (Fig. 1) and not during the lampricide/stocking period (Fig. 2) suggest that lake trout were released from competition and predation factors associated with preage I conditions. Our analysis, therefore, suggests that in Lake Superior — during the prelampricide period — interactions with other fish species were significant in determining lake trout abundance. Goddard et al. (1987) concluded that species assemblages had little or no effect on the yield of lake trout from 87 Ontario lakes. However, as opposed to our analysis, their study was based on observations of fish species at single points in time over a large number of lakes which may have masked dynamic community processes.

During the prelampricide period, high abundance of lake trout led to low abundance of lake herring with lags of 1, 2, and 3 yr possibly reflecting the predator–prey relationships between these two species. During the lampricide period, however, these relationships were not as apparent, and can be explained by observed changes in the diet of lake trout: prior to 1960 it consisted largely of lake herring; during the 1960's, rainbow smelt population increased and replaced lake herring as the major dietary item of lake trout (Dryer et al. 1965).

Lake Whitefish

The number of significant interspecific interactions of lake whitefish decreased between the prelampricide and lampricide period (Figs. 1 and 2). Following sea lamprey control, lake whitefish populations recovered, and reached nearly prelamprey levels in 1974 (Lawrie 1978). In our initial analysis of the lampricide period (Cohen and Stone 1987) we suggested that the lack of interactions was due to the benthic nature of lake whitefish. However, most interactions in the prelampricide period for lake whitefish are with lake trout (Fig. 1). Both species are often caught in nets set for each other and this is reflected in the within season interaction between lake trout and lake whitefish (Fig. 1b). However, significant interactions at longer lags, which are present in the prelampricide period but not in the lampricide period when lake trout were stocked, may reflect a biological interaction with preage I lake trout when diet overlap between the species occurs.

Lake Herring

Of the six species, lake herring exhibited the least number of intraspecific interactions (Tables 1–4 and Figs. 1 and 2). In the prelampricide period and the Intermediate I period only one significant intraspecific autoregressive coefficient was identified, as opposed to four to six for the other species. The lack of significant intraspecific coefficients could reflect (1) the

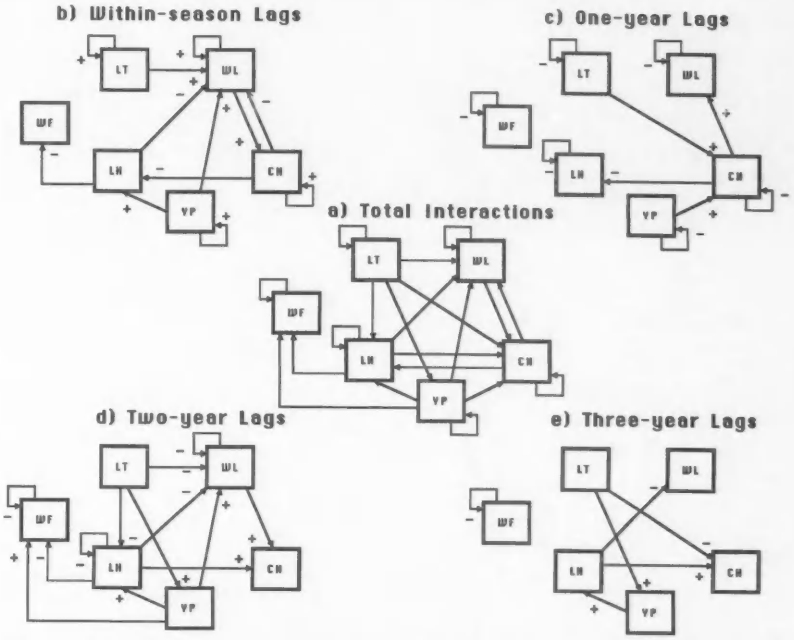

FIG. 2. Simplified web of interactions of CPUE for six commercial fish species in Lake Superior for the lampricide period according to the identified MVTS model (see the equation in the caption of Table 2). The CPUE for the species at the tail of the arrows are leading (i.e. "influencing" the CPUE) for the species at the head of the arrows; + indicate positive interactions (i.e. high CPUE forecasts high CPUE); − indicate negative interactions. The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chubs; WL, walleye; YP, yellow perch.

localized nature of the lake herring stocks which masked overfishing of lake herring in United States waters (Selgeby 1982) and/or (2) the domination of the harvest by a single age-class with recruitment independent of the adult population. Since the majority of lake herring harvest in Canadian waters was from the adjacent Thunder Bay and Black Bay, and since no evidence exists that local herring populations constitute separate stocks, the first explanation is unlikely (Jacobson et al. 1987). The lack of intraspecific interactions for lake herring appears to be due to (2) above — a density independence of the fishery and a domination of a single age-class in the harvest. Thus, Jacobson et al. (1987) found that constant recruitment was the most satisfactory model for the lake herring fisheries in Thunder Bay and Black Bay. Furthermore, in the United States fishery, a single age-class (IV) constituted 50% of all harvests during the spawning seasons of 1950–62 (Dryer and Beil 1964).

The number of intraspecific interactions for lake herring increased after 1958 (Tables 3 and 4), presumably due to a change in the seasonal pattern of lake herring harvest. In the lampricide period, commerical fishing occurred throughout the year as opposed to the traditional November–December harvest on the spawning grounds. Younger lake herring, which do not spawn, thus entered the fishery. The improvement in year round data was reflected in the increased number of intraspecific interactions.

Chubs

Historically, five species of coregonids were labelled as chubs, with the harvest concentrating on a single species at various times. The first chub to be exploited in United States waters was *C. nigripinnis*. It was fished heavily in the late 1800's and early 1900's and became commercially extinct by 1907 (Lawrie and Rahrer 1973). In the mid-1930's, *C. zenithicus* was the most common chub in the United States commercial fishery catch and from 1958 to 1965 the smaller *C. hoyi* dominated the catch of chubs (Lawrie and Rahrer 1973). Similar changes may have occurred in the Canadian fishery in Lake Superior, where in 1971, half of the harvest was *C. hoyi* and half *C. zenithicus*.

The FORECAST model for chubs in the prelampricide period included a lag of 49 mo (Table 5), which corresponded to the age (4 yr) at which the dominant chub, *C. zenithicus*, first matures (Lawrie and Rahrer 1973). However, in the lampricide

TABLE 5. Monthly lag structure of autoregressive univariate time series models for six fish species of the Canadian fisheries system in Lake Superior for data from the prelampricide and lampricide periods as identified by the SAS (1984) procedure FORECAST.

Species	Significant lags	
	Prelampricide	Lampricide
Lake trout	1, 15, 26	1, 3, 4, 6, 12, 13, 24
Lake whitefish	1, 2, 14, 15	1, 4, 12
Lake herring	1, 12, 27, 28	1, 4, 15, 27, 28
Chubs	15, 26, 49	1, 3, 4, 11, 29, 30
Walleye	1, 15, 16	1, 2, 11, 15
Yellow perch	30	1, 6, 12, 20, 29

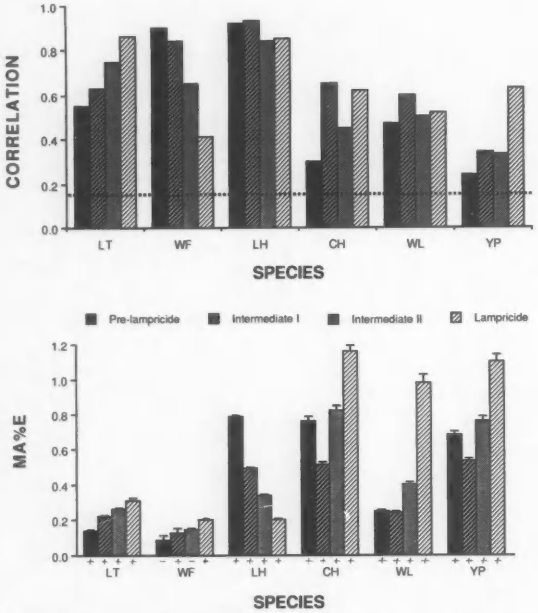

FIG. 3. Pearson correlation and MA%E between data and MVTS model fit for the six fish species for four time periods (see Tables 1–4 for the models). Broken lines indicate $p \leq 0.05$. Vertical bars indicate two standard errors as calculated from a bootstrap for the standard deviation. Positive (+) or negative (−) M%E are indicated under each column. The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chubs; WL, walleye; YP, yellow perch.

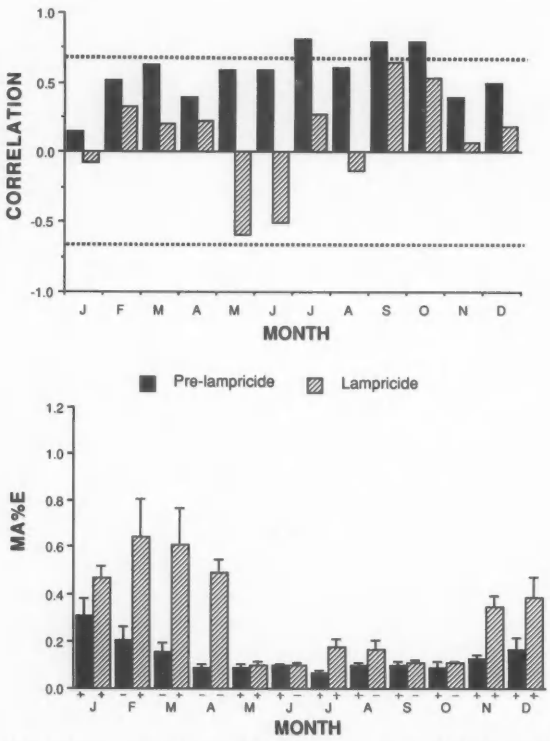

FIG. 4. Pearson correlation and MA%E between data and MVTS model fit by month for lake trout of the prelampricide period (black column) and the lampricide period (diagonal striped column). See Tables 1 and 4 for the models. Broken lines indicate $p \leq 0.05$. Vertical bars indicate two standard errors calculated from a bootstrap for the standard deviation. Positive (+) or negative (−) M%E are indicated under each column.

period, the largest lag included in the FORECAST model was 30 mo. The decrease in the largest lag may reflect the fact that *C. hoyi*, which matures at age 2, constituted 50% of the catch. The differences in the number of chub and lake herring interactions between the prelampricide and the lampricide period, therefore, may be due to the relative increase in the harvest of *C. hoyi* which, like lake herring, live in waters shallower than other chubs (Scott and Crossman 1973). Furthermore, lake herring and *C. hoyi* have similar diets (Anderson and Smith 1971).

Walleye

During the prelampricide period we did not identify interspecific interactions for walleye (Fig. 1); during the lampricide period walleye yield decreased and walleye interactions were identified with all species except lake whitefish (Fig. 2).

Walleye harvest in Black Bay, which constituted 86% of the Lake Superior harvest during 1948–76, declined rapidly to zero in 1972 after a peak yield of about 155 000 kg in 1966 (Schneider and Leach 1979). In 1965, the walleye harvest consisted of only two year-classes (Schneider and Leach 1979). Thus, species interactions became more evident, compared with the prelampricide period when more year-classes composed the harvest; i.e. if many year-classes compose the harvest, low or high abundance of a single year-class may be masked by changes in other year-classes.

Yellow Perch

Yellow perch was not a major commercial species in Lake Superior; its harvest was incidental to that of other species. We identified interspecific interactions for yellow perch and most other species (Figs. 1 and 2). Yellow perch are prey for walleye and lake trout and compete for food with lake herring and lake whitefish (Scott and Crossman 1973). Yellow perch abundance led lake herring abundance both in the prelampricide and lampricide period (Figs. 1 and 2) but the sign of the interaction changed between the periods. Similar changes occurred in Lake Huron: in the Outer Basin of South Bay, lake herring and yellow perch CPUE of a pound net sampling (from 1949–64 and 1965–85) were negatively correlated (no time lags were considered). However, a positive correlation was noted in the Inner Basin for 1965 to 1984 for a gill net sampling (Henderson and Fry 1987). We have no explanation for these changes though the quality of the data is suspect given the incidental nature of the harvest.

Model Fit

The MVTS models were correlated significantly with the data used in model identification (i.e. the model fit) and resulted in small MA%E for the three historically major commercial species: lake trout, lake whitefish, and lake herring (Fig. 3). However, changes in the models' fit occurred between periods with the direction of the change depending on the individual species. The fit of the models improved from the prelampricide period

according to the correlation criterion (Fig. 3) for lake trout, yellow perch, and chubs, decreased for lake whitefish, and changed for neither lake herring nor walleye. Based on the MA%E, all species (except lake herring) exhibited poorer fit in the later time periods (Fig. 3).

Recall that the correlation fit criterion indicates how well the trends of the model and data follow each other, and that MA%E is an indicator of how much the predicted varied from the data. Thus, increased correlation indicates an improvement in the ability of the model to track the month to month variation of CPUE whereas increased MA%E reflects the deterioration (for most species) in the closeness of fits for the predicted CPUE to the actual CPUE. Roff (1983) suggested that predictions in excess of a MA%E of 0.20 are of little practical value. Although we used MA%E only for comparative purposes between models, the MA%E was below 0.20 in some cases (Fig. 3).

The fit of the model to the data reflected not only the ability of the model but also the quality of the data (e.g. size of sampling error). Differences were expected in data quality between species. The less targeted species (i.e. yellow perch, walleye, and chubs) were expected to have poorer data and, therefore, exhibit poorer predictability (Fig. 3). Possible differences in the quality of the data (among species and time periods) must be kept in mind when placing weight on conclusions (e.g. the species interactions) made from the models. Understanding the fit of the model (i.e. residual analysis) is an important aspect of the modelling process. Because each fish species exhibited seasonal distributional characteristics, an analysis of the fit by month was necessary.

Based upon the fit criteria by month, the MVTS model for lake trout in the prelampricide period fit better than in the lampricide period (Fig. 4). During the prelampricide period, fishing effort targeted lake trout specifically. Starting in 1962, lake trout harvest was restricted to enable the recovery of its population and lake trout catch became incidental to the catch of other species. Thus, when harvest specifically targeted lake trout, the variance of CPUE was smaller (as expected) than when the catch of lake trout was incidental to the harvest of other species. In fact, the ratio of the variance of the lake trout CPUE during the lampricide period over its variance before was $F = 1.5$, $p \leq 0.01$. A better fit, therefore, is expected for less variable data, as in the prelampricide period.

As opposed to MA%E, the correlation fit criterion of the MVTS models for chubs, walleye, and yellow perch improved in most months between the prelampricide and the lampricide period. Both chubs and walleyes experienced major perturbations in the lampricide period: initiation of fishery and major stock failures, respectively. Therefore, higher MA%E values were expected. Yet, because these perturbations did not disturb monthly trends, the correlation fit remained high.

Lake whitefish CPUE was well predicted by the MVTS models in all time periods (Fig. 3) and all months. Furthermore, it was the only species whose abundance was consistently underestimated by the MVTS models in both time periods as indicated by negative M%E for all months except January and December. Knowledge of the tendency of the model to over- or underestimate is important if management decisions are to be made on predicted abundances: if the model overestimates, management decisions may need to be more conservative.

As opposed to lake trout, chubs, and lake whitefish, the identified model for lake herring during the lampricide period had a better monthly MA%E fit than in the prelampricide period. However, because of the low catch during all months except

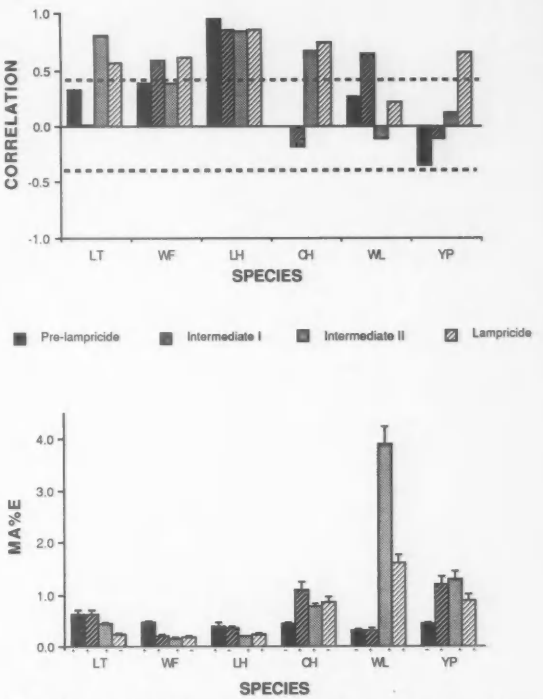

FIG. 5. Pearson correlation and MA%E between data and the 24-mo forecast of the MVTS model for the six species and four time periods (see Tables 1–4 for the models). Broken lines indicate $p \leq 0.05$. Vertical bars on the MA%E indicate two standard errors calculated from a bootstrap for the standard deviation. Positive (+) or negative (−) M%E are indicated under each column. The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chubs; WL, walleye; YP, yellow perch.

October to December in the prelampricide period, the fit of statistics for January to September for lake herring are largely irrelevant (to the fishery). Considering only October to December, the fit differed little between the prelampricide and lampricide periods for lake herring.

The fit criteria of the MVTS model and FORECAST models were similar for most species whereas the lag 12 model was consistently worse; however, the differences, in many cases, were not significant. As expected for a model that uses only its own past history, the FORECAST models generally included more lags than the MVTS models. Furthermore, the FORECAST models confirmed the lag structure identified for the MVTS models (compare Tables 1–4 with Table 5). Such models do not, however, shed light on community structure and dynamics.

Forecastability

Good fit does not necessarily imply accurate forecasts. For example, although the MVTS models for lake whitefish fit better in the prelampricide than in the lampricide period (Fig. 3), the forecasts were equal if not better for the lampricide period (Fig. 5). The differences reflected large perturbations to the fishery system (e.g. sea lamprey control, lake trout harvest restrictions, stocking) at the end of the prelampricide period and fewer disturbances following the lampricide period. These

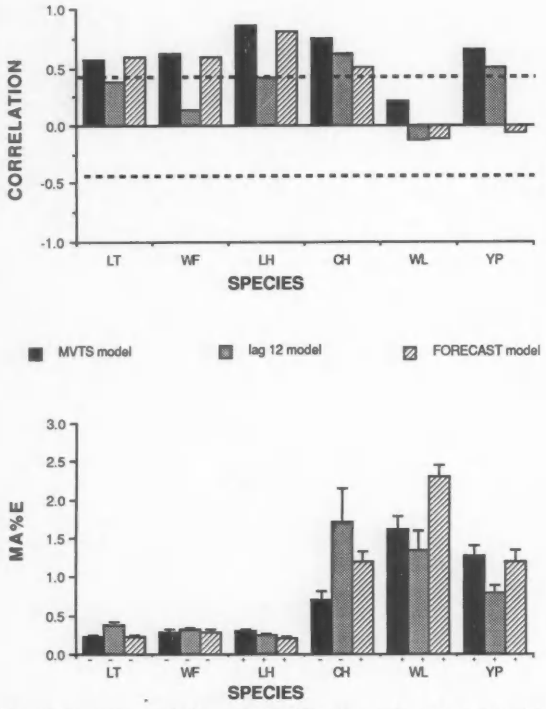

FIG. 6. Pearson correlation and MA%E between the data and the 24-mo forecast of the MVTS, lag 12, and FORECAST models for the six species during the lampricide period. See Tables 4 and 5 for the models. Broken lines indicate $p \leq 0.05$. Vertical bars on the MA%E indicate two standard errors calculated from a bootstrap for the standard deviation. Positive (+) or negative (−) M%E are indicated under each column. The species are LT, lake trout; WF, lake whitefish; LH, lake herring; CH, chubs; WL, walleye; YP, yellow perch.

differences in forecastability were true for other species, e.g. walleye 24-mo forecasts were better (higher correlation and lower MA%E) immediately following the prelampricide period than during the lampricide period. Similar conclusions were reached with forecast periods other than 24 mo (not shown).

The forecasts of the MVTS and FORECAST models were similar for lake trout, lake whitefish, and lake herring and the forecasts for the lag 12 model were poorer (Fig. 6). For chubs, walleye, and yellow perch, MVTS models had the highest correlation fit; however, the lag 12 models had generally smaller MA%E fit. For these species and both statistics, FORECAST models had the worst fit. This poor fit by the FORECAST models may be due to the perturbations that had occurred in the fishery during the lampricide period; i.e. FORECAST models relied on data from single time series which included the large perturbations. Consequently, the lag 12 model only reflected the most recent past; i.e. the last year of data used in model identification was similar to the period forecasted and did not include data before the perturbation. Thus, one of the disadvantages of using FORECAST models is their tendency to include many lags, and therefore to include large inertia.

The choice of the best model for forecasting among the three models is not obvious. It therefore depends on other model qualities such as the purpose or the ease of use of the model. The lag 12 model requires only knowledge of the previous year's CPUE. The FORECAST model, however, requires data from many previous years. Multivariate time series models require more data (e.g. many time series) than the previous two models, and knowledge of the iterative procedures involved in the identification process. For any model choice, it is important to understand how its input requirements and its outputs (parameters) reflect characteristics other than those identified for the data. Therefore, comparison of results from several models, as done here, should be undertaken whenever possible. This is particularly true when the purpose of modelling is taken into account. For example, when only forecasts are desired, and when the system is little perturbed, FORECAST and lag 12 models may suffice. When a deeper understanding of the system is desired, MVTS models are more powerful.

Conclusions

The identified system structure of the Lake Superior fishery changed between the period prior to effective sea lamprey control and the period of effective control. Direct effects of the control were difficult to ascertain. However, the identified interactions appear to have been influenced by other perturbations related to the control (e.g. increased stocking efforts for lake trout).

Multivariate time series analysis was an effective tool in elucidating (or raising questions about) species interactions. Intraspecific and known predator–prey relationships were identified. These interactions are the easiest possibilities for the modeller to hypothesize given the model structure and the known biology of the fish species. However, the models also encapsulated other system's characteristics (e.g. fishers' behaviour or data quality changes) which must be considered.

Univariate time series methods appear to be as effective as the multivariate time series methods for forecasting abundance. However, the univariate models generally required longer lags than the MVTS models (as expected) and do not provide information about community structure.

Information extracted by the MVTS models indicate the value of the Canadian Lake Superior commercial fisheries data. The quality of the data varied among species and time periods. Residual analysis assesses the quality of the data and is necessary to help differentiate between ecologically related interactions and those related to other system characteristics.

Continuation of the collection of data and analysis of the Canadian Lake Superior commercial fisheries will be a worthwhile endeavour for the understanding of the Lake Superior fisheries. Similar analysis of United States fisheries with its different influences (e.g. quotas and fishers' behaviour) would lead to an improved understanding of the Lake Superior fisheries as a whole.

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Effect of Nutrient Additions on Lower Trophic Levels of an Oligotrophic Lake with a Seasonal Deep Chlorophyll Maximum

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Shortreed, K. S., and J. G. Stockner. 1990. Effect of nutrient additions on lower trophic levels of an oligotrophic lake with a seasonal deep chlorophyll maximum. Can. J. Fish. Aquat. Sci. 47: 262–273.

Inorganic nitrogen and phosphorus were added to the surface of selected areas of Sproat Lake, Vancouver Island, British Columbia for varying periods in 1985 and 1986. The lake is monomictic, oligotrophic, and for much of each year has a deep chlorophyll maximum (DCM) located near the bottom of the euphotic zone (20–25 m). Epilimnetic chlorophyll concentrations are low (ca. 0.5 $\mu g \cdot L^{-1}$) in summer, and DCM concentrations are from three to 10 times higher. The diatom *Rhizosolenia eriensis* was a dominant species in the epilimnion in spring and at the DCM for much of the year, but was rare in the epilimnion during summer, and consequently was not affected by the nutrient additions. *Cyclotella* spp. were also abundant in spring, were a prominent component of the DCM, and increased in abundance during nutrient additions. The cyanobacterium *Synechococcus* was the dominant member of the autotrophic picoplankton community and during the nutrient additions densities reached 300 000$\cdot mL^{-1}$ (a 10-fold increase). Bacterioplankton numbers also increased during nutrient additions, at times exceeding $3.0 \times 10^6 \cdot mL^{-1}$. The DCM was formed and maintained by sinking cells, by occasional active photosynthesis at the DCM, and by an increase in chlorophyll/cell.

Du phosphore et de l'azote inorganiques ont été ajoutés en certains points à la surface du lac Sproat sur l'île de Vancouver en Colombie-Britannique, au cours de périodes de longueur variable en 1985 et 1986. Le lac est monomictique, oligotrophe et, pour la majeure partie de l'année, présente un maximum de chlorophylle profond (MCP) situé près du fond de la zone euphotique (20 à 25 m). Les concentrations de chlorophylle dans l'épilimnion sont faibles (environ 0,5 $\mu g \cdot L^{-1}$) en été et les concentrations de chlorophylle dans le MCP atteignent trois à 10 fois ce nombre. La diatomée *Rhizosolenia eriensis* était une espèce dominante dans l'épilimnion au printemps et dans le MCP la majeure partie de l'année, mais était rare dans l'épilimnion en été, et n'a donc pas été touchée par les ajouts d'éléments nutritifs. *Cyclotella spp.* étaient également abondants au printemps, constituaient une composante importante du MCP et augmentaient en abondance au cours des ajouts d'éléments nutritifs. La cyanobactérie *Synechococcus* était le membre dominant du picoplancton autotrophe et, au cours des ajouts d'éléments nutritifs, les densités ont atteint 300 000$\cdot mL^{-1}$ (10-fois plus). L'effectif bactérioplanctonique a également augmenté au cours des ajouts d'éléments nutritifs et excédait par moment $3{,}0 \times 10^6 \cdot mL^{-1}$. Le MCP résultait de l'action de cellules à flottabilité négative, d'une photosynthèse active par moment à cet endroit et d'une augmentation du taux de chlorophylle par cellule. Mots clés : oligotrophe, monomictique, azote, phosphore, bactérie, photosynthèse, maximum de chlorophylle profond, picoplancton, diatomés.

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For the past decade we have been carrying out large-scale nutrient additions on a number of oligotrophic lakes located near the west coast of Canada (Stockner and Shortreed 1985; 1988). These lakes are of considerable economic importance because they are nursery areas for juvenile sockeye salmon (*Oncorhynchus nerka*), commercially the most valuable salmonid species on the west coast of North America. Nutrient additions to a number of these lakes have been successful in the general objective of increasing sockeye numbers (Hyatt and Stockner 1985; Stockner 1987). In this particular investigation, which took place on Sproat Lake, Vancouver Island, British Columbia, we studied a number of aspects of the lake's plankton (including bacterio- and picoplankton) communities both before and during nutrient additions. A considerable amount of research in the past several years has focused on various aspects of phototrophic picoplankton ecology and physiology, and a substantial body of literature now exists (See reviews by Stockner and Antia 1986; Platt and Li 1987; Fogg 1986). However, to date little work has been done on the effects of varying nutrient loads on picoplankton, particularly in large lakes, and this study provided the opportunity to compare picoplankton response with that of other members of the phytoplankton community.

Deep chlorophyll maxima are common in the oceans as well as in numerous lakes, and a number of hypotheses have been put forward to explain their development and maintenance (Cullen 1982; Moll and Stoermer 1982; Pick et al. 1984). The existence of a pronounced deep chlorophyll maximum (DCM) in Sproat Lake provided the additional opportunity of determining the contribution of various components of the phytoplankton community to its development and maintenance, and also of determining the effects of increased nutrient loading on the DCM.

The study reported here had three main objectives: first, to determine effects of nutrient additions on the distribution, density, and photosynthetic rates of the lake's phytoplankton com-

munity; second, to examine effects of nutrient additions on density and distribution of the bacterioplankton; and third, to estimate relative importance of various factors contributing to formation and maintenance of the DCM.

Description of Study Lake

Sproat Lake is located in the south-central portion of Vancouver Island, an area with warm, dry summers and cool, wet winters. The lake is warm monomictic, with a mean depth of approximately 59 m and a theoretical water residence time of 8 yr. Littoral areas are very small (Shortreed et al. 1984), and the lake is divided into four distinct basins which are separated by shallow sills (Fig. 1). The surrounding topography and orientation of the lake act to shield it from prevailing winds, with the result that there is relatively little wind-induced vertical mixing. The surrounding drainage basin has shallow, sandy soils underlain by impervious igneous rock which result in generally low dissolved ion concentrations. The lake is an important nursery area for sockeye salmon, which spend 1–2 yr in the lake prior to seaward migration.

Methods

An aqueous solution of ammonium nitrate and ammonium phosphate was added once weekly to the surface of Taylor Arm (TA) of Sproat Lake from May 13 to September 9 (18 wk) of 1985 and from May 20 to July 7 (7 wk) of 1986. Phosphorus loading rates were 3.0 mg $P \cdot m^{-2} \cdot wk^{-1}$ in 1985 and 5.6 $mg \cdot P \cdot m^{-2} \cdot wk^{-1}$ in 1986 (areal loading rates were calculated using the area of TA, not the area of the whole lake). No nutrients were added to Two Rivers Arm (TRA). The nitrogen to phosphorus (N:P) atomic ratio of added nutrients was held constant at 50:1.

Frequency of sampling ranged from weekly to monthly depending on the time of year, but for much of the study the lake was sampled once every 2 wk. Data presented here were collected from one site in TA and one in TRA in 1984–86 (inclusive). In the two years of fertilization sampling dates were scheduled to occur 3–4 d after a nutrient application. Temperature profiles were collected using an Applied Microsystems Ltd. Model STD-12 conductivity, temperature, and depth meter, calibrated against an NBS-calibrated mercury thermometer. Photosynthetically active radiation (400–700 nm) was determined using a Li-Cor Model 185A light meter equipped with a Model 192S underwater quantum sensor. These data were used to calculate compensation depths and vertical light extinction coefficients. Daily solar radiation was measured with a Model 190S quantum sensor and recorded on a Li-Cor Model 550 printing integrator.

An opaque 6-L Van Dorn water sampler was used to collect all water samples, usually between 0900 and 1100 h. Water at 10 depths from the surface to below the DCM was collected for analysis of selected chemical variables, phytoplankton biomass, and phytoplankton species composition; in situ photosynthetic rates were determined from the same depths. Depths

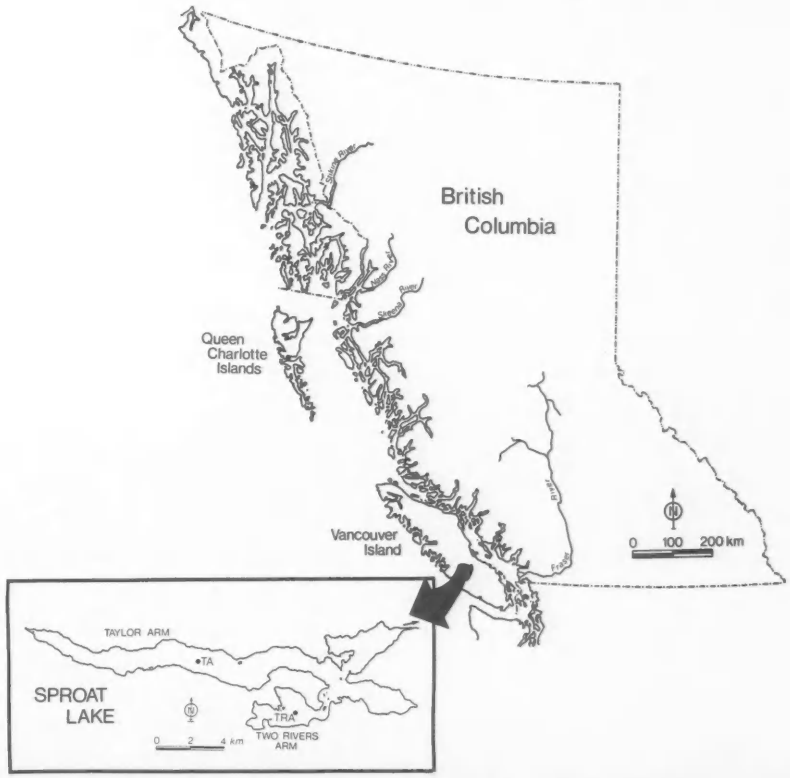

FIG. 1. Map of British Columbia and Sproat Lake, with sampling locations indicated.

to be sampled were selected after observing vertical profiles of in vivo fluorescence (IVF), which were collected using a Turner Designs Model 10 fluorometer, hose, and pump from the start of the study until June 1986, and an Elektro-Optik Juan F. Suarez in situ fluorometer for the remainder of the study.

All reported chemical analyses were done according to methods described by Stephens and Brandstaetter (1983) and Stockner and Shortreed (1985). Water for dissolved nutrient analyses was filtered through ashed Whatman GF/F filters which were rinsed with both distilled deionized water (DDW) and sampled immediately prior to filtration. Filtered water was stored in clean glass and polyethylene bottles and kept cold and dark prior to analysis. Nitrate was determined by converting to nitrite by cadmium reduction. Water for total phosphorus (TP) analysis was collected in clean, screw-capped, glass test tubes, and TP was later determined using a molybdenum blue method after persulfate digestion. Samples for particulate phosphorus (PP), particulate carbon (PC), and particulate nitrogen (PN) analyses were obtained by filtering water through Whatman GF/F filters. Filters for PC and PN determinations were frozen after desiccation. The method of Stainton et al. (1977) was used for PP determinations; PC and PN were determined on a Perkin Elmer Model 240XA Elemental Analyzer.

Samples for chlorophyll a determination were collected on either Millipore AA filters or on Nuclepore filters of preselected pore sizes, desiccated, frozen, and later analyzed fluorometrically after maceration in 90% acetone. In situ photosynthetic rates were determined by filling 125-mL glass bottles (clear and lightproof) with water from each sampling depth, inoculating with a sodium bicarbonate solution containing ^{14}C, and incubating for 1.5–2 h at the original sampling depths. Incubations usually commenced between 0900 and 1000 h. After the incubations, samples were filtered onto 0.2-μm Nuclepore filters and placed in scintillation vials containing a tissue solubilizer. For a portion of the study, 3.0-μm pore size Nuclepore filters were also used in an effort to estimate picoplankton photosynthetic rates. Scintillation cocktail was later added to the vials and samples were counted in a Packard Model 4530 liquid scintillation counter. Dissolved inorganic carbon (DIC) concentrations were determined using the potentiometric method of APHA (1980). Photosynthetic rates were calculated using Strickland's (1960) equation. Phytoplankton larger than the picoplankton size fraction (>3 μm maximum linear dimension) were identified and enumerated using a Wild inverted microscope equipped with phase optics. These techniques did not permit differentiation of autotrophic and heterotrophic microflagellates. Picoplankton were collected on a 0.2-μm pore size Nuclepore filter at a vacuum pressure (<15 cm Hg, and enumerated with a Zeiss epifluorescent microscope using methods described in MacIsaac and Stockner (1985).

At most sampled depths a test tube rinsed with 95% ethanol was rinsed and then filled with water for bacterial enumeration. In the laboratory, 5 mL was filtered onto a 25-mm diameter, 0.2-μm Nuclepore membrane filter counter-stained with Irgalan Black. Filters were removed when just dry and placed onto a 9-cm divided petri dish lined with Whatman filter paper, air-dried at room temperature (approximately 20°C) and stored. Bacteria were later counted under epifluorescence using the acridine orange direct count (AODC) method as modified by MacIsaac et al. (1981). Bacteria size was not measured in this study.

All isoline figures in this report were created using SAS software on a VAX minicomputer.

Results

Thermal stratification commences in April at Sproat Lake and in most years is maintained until November. The generally calm conditions which predominate for much of the year contribute to development of a strong thermocline which occurs at a depth of 8 to 10 m during summer and early fall, and surface water temperatures exceed 20°C for much of the summer (Fig. 2). In later sections of this report epilimnetic averages will consist of data from the surface to the thermocline, and hypolimnetic averages from the thermocline to 30 m. Sproat Lake generally has high water clarity, with vertical extinction coefficients of 0.17 to 0.24 m^{-1} in summer, and a range in compensation depths of 18 to 28 m that results in a euphotic depth often two times deeper than the average thermocline depth. During nutrient additions, extinction coefficients in TA were slightly higher, and ranged from 0.19 to 0.28 m^{-1}, and compensation depths were lower (range: 15–24 m).

The pH of Sproat Lake is circumneutral, and dissolved nutrients are present in generally very low concentrations (Table 1). Total phosphorus levels ranged from below our analytical detection limit of 1 $\mu g \cdot P \cdot L^{-1}$ to a high of 4 $\mu g \cdot L^{-1}$ and were generally <2 $\mu g \cdot L^{-1}$. Temporal or spatial trends in phosphorus concentration were not apparent. Nitrate concentrations were 30–40 $\mu g \cdot N \cdot L^{-1}$ in winter, and in the surface waters were <1 $\mu g \cdot L^{-1}$ during summer, with a distinct nitracline present below the thermocline at 15–20 m (Fig. 3). During nutrient additions in TA, epilimnetic nitrate concentrations were slightly higher (2–5 $\mu g \cdot L^{-1}$) on dates that we sampled the lake, which were generally 3 d after a nutrient application. Ammonia concentrations were almost always below our detection limit of 4 $\mu g \cdot N \cdot L^{-1}$.

Epilimnetic chlorophyll concentrations exhibited peaks in April or May, and then quickly declined to unfertilized summer levels of approximately 0.5 $\mu g \cdot L^{-1}$ (Fig. 4). Epilimnetic chlorophyll concentrations were generally lower in summer than in winter, except during periods of fertilization. In the first year of nutrient additions (1985), epilimnetic summer chlorophyll concentrations in TA were approximately double those in TRA and were also double TA concentrations in an unfertilized year (1984). During nutrient applications in 1986, epilimnetic chlorophyll concentrations increased rapidly to >1 $\mu g \cdot L^{-1}$, and declined after nutrient additions ceased on July 7, 1986 (Fig. 4, 5). Chlorophyll levels at the DCM ranged from three to 10 times higher than those in the epilimnion.

The DCM generally commenced development in April at a depth of 10–15 m, and usually occurred in a relatively broad band. It slowly deepened to 20–25 m by July, and persisted until October (Fig. 4). While this pattern occurred in TA in the first year of nutrient additions (1985), when loads to TA were nearly doubled (1986), the seasonal pattern was altered. Both TA (fertilized) and TRA (unfertilized) had similar IVF profiles until late May, and until late June the shape of the profiles was similar in both arms. In July, IVF profiles in TRA remained relatively constant, with a broad DCM at 18–25 m. However, in July the DCM in TA was replaced by two shallower IVF peaks located above and below the thermocline (Fig. 5). On July 7, 1986 we terminated nutrient additions to TA, but the double peak persisted for several weeks as chlorophyll concentrations gradually decreased and water transparency increased. Through this transition period the subsurface chlorophyll peaks slowly deepened and became less pronounced. By August 11,

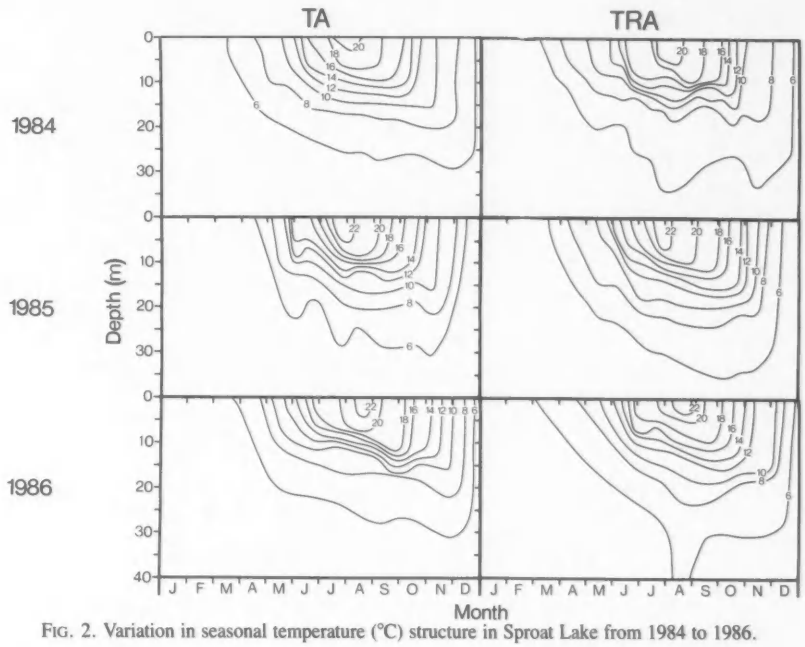

FIG. 2. Variation in seasonal temperature (°C) structure in Sproat Lake from 1984 to 1986.

TABLE 1. Comparison of growing season (May–October) averages of salient physical, chemical, and biological data for TA (fertilized-F and unfertilized-UF) and TRA during fertilized and unfertilized conditions. Data are from 1984 for unfertilized TA, from 1985 for fertilized TA, and are averages of 1984 and 1985 for TRA. Epilimnetic (Epi) data are averages of 0–10 m and DCM data are averages of 15–25 m.

	TRA-UF		TA-UF		TA-F	
Variable	Epi	DCM	Epi	DCM	Epi	DCM
Surface temperature (°C)	16.9		15.8		17.1	
Epilimnion depth (m)	11.1		10.5		11.1	
Compensation depth (m)	22.5		21.1		20.0	
Nitrate ($\mu g \cdot L^{-1}$)	1.8	8.4	3.7	9.2	5.2	7.9
Particulate nitrogen ($\mu g \cdot L^{-1}$)	21.0	29.0	21.5	27.4	24.9	22.2
Total phosphorus ($\mu g \cdot L^{-1}$)	1.4	1.6	1.2	1.4	1.5	1.2
Particulate phosphorus ($\mu g \cdot L^{-1}$)	0.77	1.19	0.66	1.13	1.13	1.15
Particulate carbon ($mg \cdot L^{-1}$)	0.19	0.23	0.20	0.21	0.24	0.22
Bacteria number (No. $\times 10^6 \cdot mL^{-1}$)	0.74	0.82	0.68	0.85	0.96	0.66
Total chlorophyll ($\mu g \cdot L^{-1}$)	0.65	2.27	0.68	2.09	1.08	1.94
Total photosynthesis (mg $C \cdot m^{-3} \cdot h^{-1}$)	0.53	0.28	0.68	0.30	0.91	0.29

the DCM had reestablished itself, but at a slightly lesser depth (Fig. 5).

In situ photosynthetic rates did not exhibit distinct seasonal trends, but rates were substantially higher during fertilization (Fig. 6). In 1985 average epilimnetic rates in TA slowly increased from 0.5 mg $C \cdot m^{-3} \cdot h^{-1}$ in May to >1.5 mg $C \cdot m^{-3} \cdot h^{-1}$ in August, and then decreased rapidly when nutrient additions ended. A similar pattern occurred in 1986, although the increase was more rapid, with a photosynthetic peak occurring in late June, and a rapid decrease commensurate with the decline in chlorophyll concentrations when nutrient additions ended. Fractionated photosynthetic rate estimates indicated that the relative contribution of the <3 μm fraction was quite variable, but averaged about 50% of total photosynthesis, with no detected changes in relative importance during nutrient additions. Vertical profiles of photosynthesis were substantially affected by the nutrient additions. When nutrients were not being applied, photosynthetic rates tended to be similar from the surface to 15–20 m; and when peaks were present, they usually occurred at depths >10 m (Fig. 6). During fertilization, prominent photosynthetic peaks occurred at depths <10 m and summer epilimnetic photosynthetic rates comprised an average of 71% of total photosynthesis, contrasted to 57% when the lake was not being fertilized. Photosynthetic rates at the DCM were always much lower than rates nearer the surface, and on many occasions were undetectable. Viability of phytoplankton at the DCM was tested by collecting water from the DCM and incubating it near the surface. These samples had substantially higher photosynthetic rates than samples of DCM water incubated at depth and also had higher photosynthetic rates than

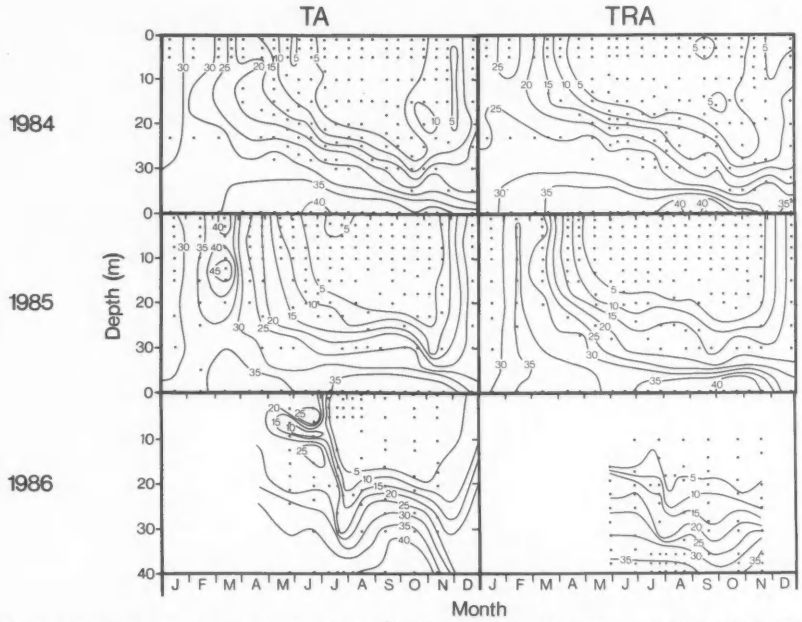

FIG. 3. Variation in nitrate concentration ($\mu g \cdot L^{-1}$) in TA and TRA. Nutrients were added to TA for 18 wk (May to September) in 1985 and for 7 wk (May to July) in 1986.

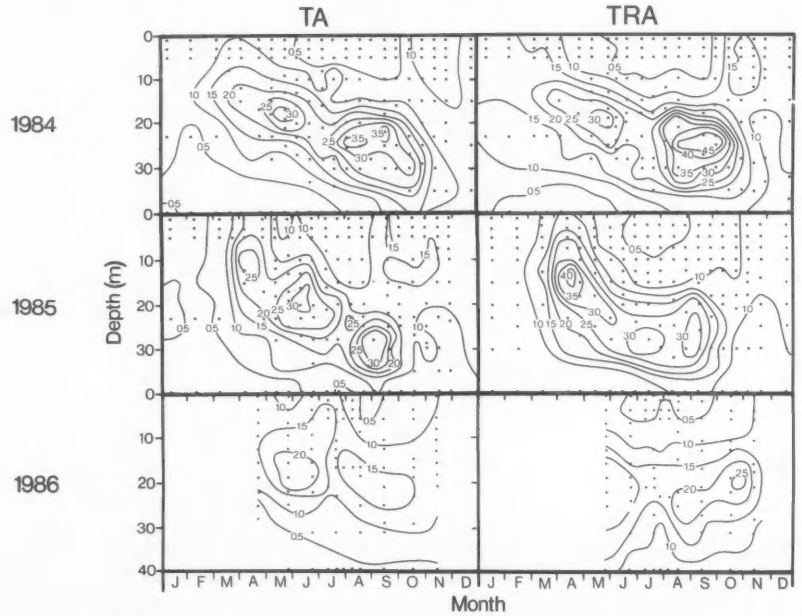

FIG. 4. Changes in chlorophyll concentrations ($\mu g \cdot L^{-1}$) in TA and TRA during the study. Nutrients were added to TA for 18 wk (May to September) in 1985 and for 7 wk (May to July) in 1986.

epilimnetic samples, but epilimnetic samples had highest assimilation efficiencies (Table 2).

Free-living pelagic bacteria numbers ranged from winter lows of about $5.0 \times 10^5 \cdot mL^{-1}$ to highs of around $1.0 \times 10^6 \cdot mL^{-1}$ in autumn in untreated basins and years (Fig. 7). In 1984 bacteria densities tended to be higher in the hypolimnion than in the epilimnion, and their vertical distribution within the upper 40 m was relatively uniform, but on most occasions slightly higher numbers were associated with the DCM (Fig. 7). Nutrient additions to TA in 1985 markedly increased bacterial numbers, especially in the epilimnion, where densities $>3.0 \times 10^6 \cdot mL^{-1}$ were reached in early September (Fig. 7).

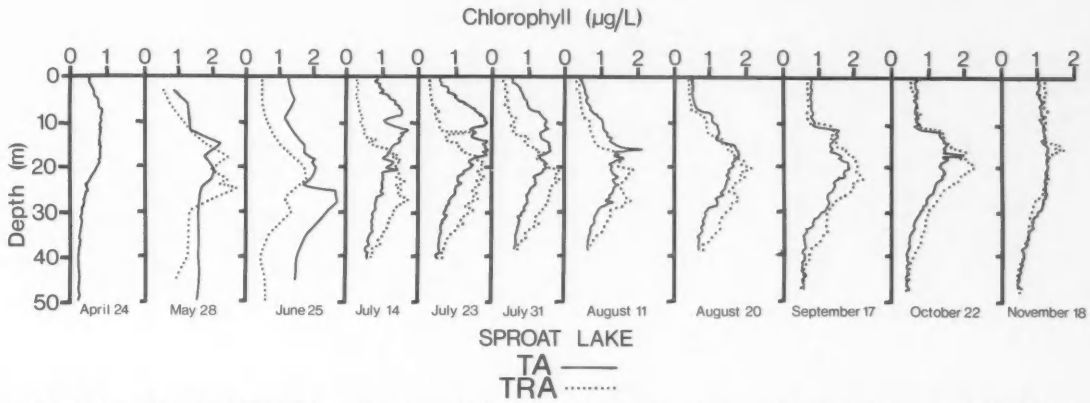

FIG. 5. Variation in vertical profiles of chlorophyll concentration (derived from IVF profiles) in 1986. Nutrients were added to TA for 7 wk (May 20 to July 7) in 1986.

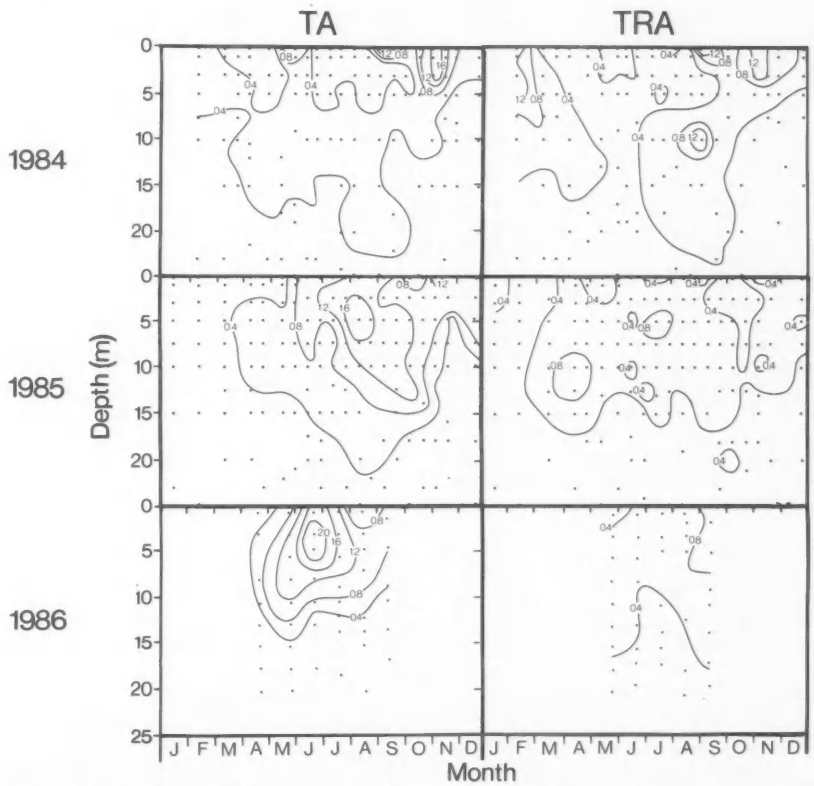

FIG. 6. Seasonal photosynthetic rates (mg $C \cdot m^{-3} \cdot h^{-1}$) during the study. (Note different scale on vertical axis in this figure).

Phytoplankton community structure and succession in Sproat Lake was typical of many oligotrophic lakes, with a spring peak of microphytoplankton (>20 µm) in the epilimnion, followed by a rapid decline in June. Epilimnetic microphytoplankton comprised 90–99% of phytoplankton volume and 60–65% of chlorophyll in spring and early summer, and declined to 60–70% of volume and 40–45% of chlorophyll by fall. In the hypolimnion, microphytoplankton comprised over 90% of phytoplankton biomass for much of the stratified period. An average of 73% of the chlorophyll occurred in the microphytoplankton fraction in the hypolimnion (range, 62–75%). The large diatom *Rhizosolenia eriensis* was the dominant member of the microphytoplankton throughout the study. A peak in average epilimnetic numbers of $>2000 \cdot mL^{-1}$ generally occurred in May or June, followed by a rapid decline until the end of July. From this time on epilimnetic numbers were very low (Fig. 8). Com-

TABLE 2. Results of a photosynthesis experiment at TRA on July 24, 1986 to test the response of DCM phytoplankton to increased light and temperature. On this date temperatures at 5 and 20 m were 19.4 and 7.2°C, respectively, and the compensation depth was 21.4 m.

Treatment	Replicate	Production (mg C·m^{-3}·h^{-1})	Assimilation efficiency (mg C·mg Chl^{-1}·h^{-1})
5 m water incubated at 5 m	1	0.55	
	2	0.62	
	3	0.48	
	4	0.48	
	Mean	0.53	0.98
20 m water incubated at 20 m	1	0.29	
	2	0.29	
	3	0.25	
	4	0.16	
	Mean	0.25	0.14
20 m water incubated at 5 m	1	0.69	
	2	0.68	
	3	0.72	
	4	0.70	
	Mean	0.70	0.38

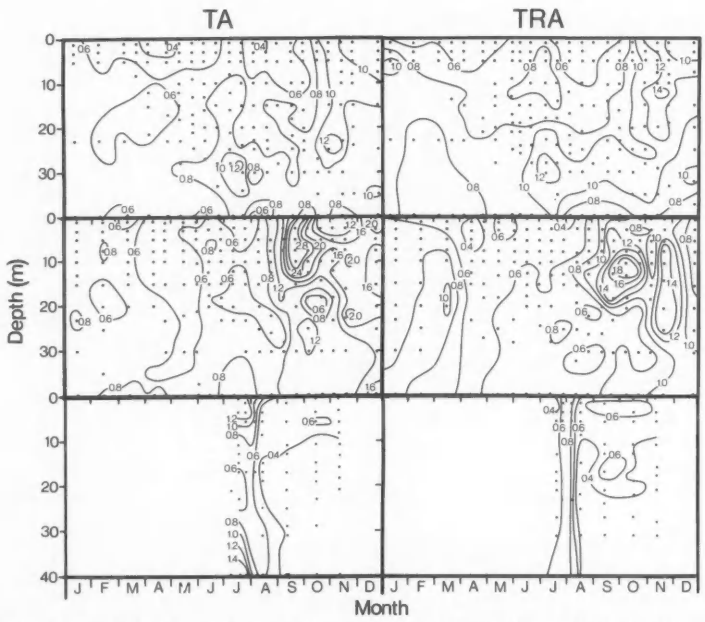

FIG. 7. Variation in bacterioplankton numbers (millions·mL^{-1}) in TA and TRA from 1984–86. TA was unfertilized throughout the study and nutrients were added to TA for 18 wk (May to September) in 1985 and for 7 wk (May to July) in 1986.

mensurate with the decline of *R. eriensis* were increases in hypolimnetic numbers, usually to average concentrations >3000·mL^{-1}. In summer, vertical profiles of *R. eriensis* density closely paralleled the DCM, with a distinct hypolimnetic peak in density (Fig. 8). Nutrient additions had little effect on *R. eriensis*, with similar concentrations present in summer in both fertilized and unfertilized years. However, the elimination of the DCM during fertilization in 1986 was accompanied by the elimination of the hypolimnetic peak in *Rhizosolenia* numbers, and the redevelopment of the peak in late summer. Microflagellate numbers were lower in 1985 than in 1984 in both lake basins, although the decline was more pronounced in hypolimnetic populations. *Cyclotella* spp. (primarily *C. kutzingiana* and *C. stelligera*, with fewer numbers of *C. ocellata* and *C. comta*) were numerically the most abundant diatoms in Sproat Lake. Under unfertilized conditions, succession of *Cyclotella* was

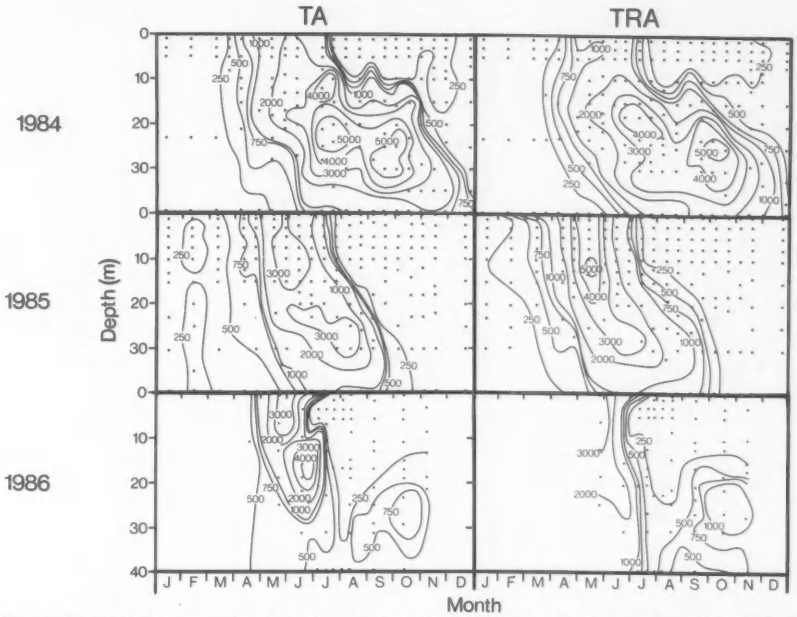

FIG. 8. Seasonal changes in density and vertical distribution of *Rhizosolenia* (numbers·mL^{-1}) in both lake basins. Nutrients were added to TA for 18 wk (May to September) in 1985 and for 7 wk (May to July) in 1986.

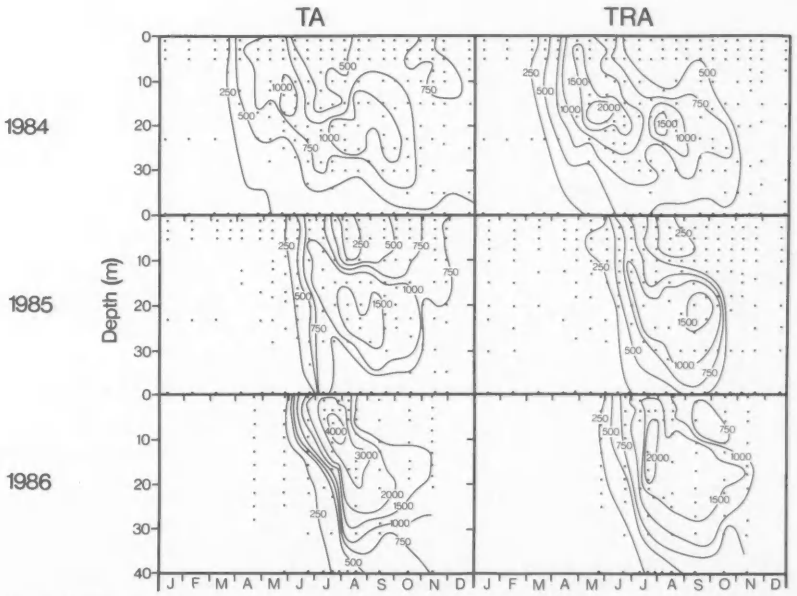

FIG. 9. Seasonal variation in *Cyclotella* spp. in Sproat Lake from 1984–86. Nutrients were added to TA for 18 wk (May to September) in 1985 and for 7 wk (May to July) in 1986.

similar to that of *Rhizosolenia*, with a spring peak in the epilimnion followed by increases below the thermocline, and maximum numbers occurring at the DCM from early July until fall (Fig. 9). During summer, epilimnetic concentrations of *Cyclotella* tended to be higher than those of *Rhizosolenia*. During the fertilized period in 1986, epilimnetic concentrations of *Cyclotella* increased to densities of up to 5000·mL^{-1}, and development of maximum numbers at the DCM was delayed until late July or early August.

The coccoid cyanobacteria *Synechococcus* sp. was the dominant member of the autotrophic picoplankton community and the most abundant phytoplankter in Sproat Lake, with very low

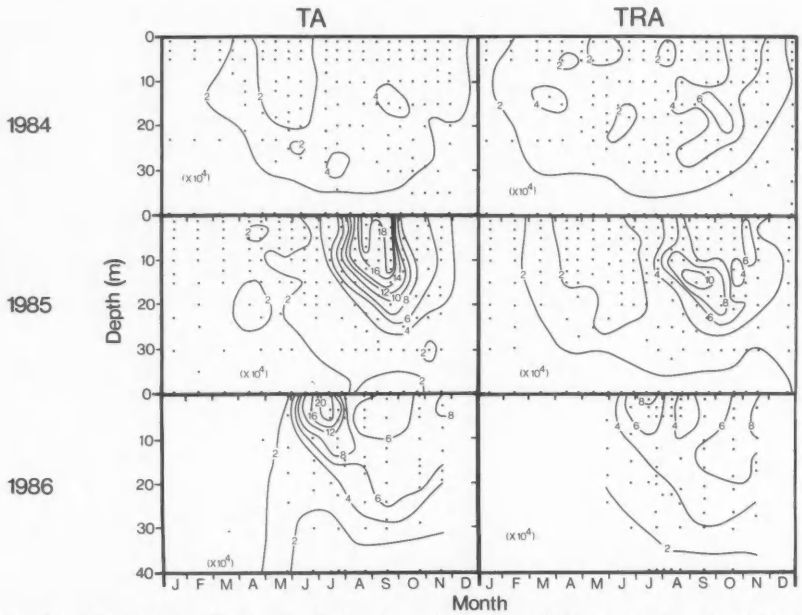

FIG. 10. Variation in picoplankton density (numbers·mL^{-1}) in TA and TRA during the study. Nutrients were added to TA for 18 wk (May to September) in 1985 and for 7 wk (May to July) in 1986.

numbers of coccoid eucaryotic picoplankters present. In unfertilized years and lake basins highest algal picoplankton numbers (75 000–100 000 cells·mL^{-1}) usually occurred in September or October of each year, with lows (<10 000 cells·mL^{-1}) occurring from November to March. Vertical profiles of picoplankton abundance did not exhibit distinct subsurface maxima for much of the year, but peaks in density at 12–15 m at the base of, or just beneath the thermocline occurred in late summer or early fall (Fig. 10). During nutrient additions, peaks in epilimnetic algal picoplankton numbers were substantially higher (>200 000 cells·mL^{-1}), occurred near the surface, and the late summer subsurface peak did not occur (Fig. 10). In both fertilized years (1985–86), epilimnetic picoplankton numbers declined abruptly upon termination of nutrient additions (September 1985 and July 1986).

Discussion

The distinctive physico-chemical characteristics of Sproat Lake interact to produce a number of interesting biological features, including epilimnetic chlorophyll concentrations that have their annual minima in the summer months and maxima in late-fall and winter, and the presence of a pronounced DCM during the summer stratification period. The mild climate and generally light winds contribute to early formation of a strong, stable seasonal thermocline at a depth of 8–10 m. These thermal properties and the low nutrient loading, especially during the low-flow summer period, result in rapid depletion of epilimnetic nitrate by as early as April in some years, and epilimnetic nutrient depletion may continue until well into the month of October. The clear waters of Sproat Lake result in a euphotic zone which is often two-fold greater than the depth of the thermocline. Therefore there is substantial hypolimnetic photosynthesis, resulting in depletion of nitrate for several metres below the thermocline, and a pronounced nitracline which is generally located near the base of the euphotic zone and above the DCM (Fig. 3). Because the lake has such a strong thermocline, and is steep-sided with a very small littoral zone, this hypolimnetic zone of nutrient-depleted water appears to be an effective barrier to any significant vertical flux of nutrients to the epilimnion (internal loading). Together with the warm, dry summers which produce low stream flows and consequently little external loading for much of the year, this lack of internal loading results in exceptionally low summer phytoplankton biomass in the epilimnion, high water clarity and extreme nutrient limitation, with a resulting high demand for both nitrogen and phosphorus by phytoplankton for much of the growing season (Suttle et al. 1988; Suttle and Harrison 1988; Stockner and Shortreed 1988).

Nutrients and Photosynthesis

Because of the high demand for nutrients in the epilimnion of Sproat Lake, it is reasonable to expect that virtually all nutrients added during the study would at least initially be taken up by the phytoplankton community, and result in 'new' production. One method of examining this question is to estimate the amount of increased production which could result from the nutrient additions. During 1985, 0.174 μM P and 8.71 μM N were added to TA over 18 wk (based on an average epilimnion depth of 10.1 m during this period). Assuming a phytoplankton C:N:P ratio of 103:16:1 (Redfield et al. 1963), these added nutrients should have produced an additional 17.9 μM C.

During this same period, epilimnetic photosynthesis averaged 0.990 μM C·d^{-1} in TA and 0.625 μM C·d^{-1} in TRA, an increase of 0.365 μM·d^{-1} in TA. Over the 18-wk period of nutrient additions, this resulted in an estimated additional 46.2 μM C produced. The ratio of this 'additional' C with fertilizer N and P was 265:50:1. Average particulate C:N:P ratios in TA

and TRA (537:49:1 and 756:62:1, respectively) were considerably higher than the Redfield ratio of 103:16:1 (Redfield et al. 1963), and are indicative of severe nutrient limitation (Healey and Hendzel 1980), with the unfertilized arm (TRA) exhibiting a greater degree of limitation. Assuming that TRA can be considered an adequate control for TA, and that the allochthonous component of the particulate pool is similar in the two arms, differences in particulate C, N, and P concentrations between the two arms of the lake should be indicators of increased biomass as a result of fertilization. During the period of nutrient additions in 1985, average epilimnetic concentrations of particulate C, N, and P in TA were 5.2, 0.57, and 0.019 μM (respectively) higher than those in TRA, which resulted in a ratio of 274:30:1, still higher than the Redfield ratio and indicative of nutrient limitation. The similar C:P ratios of 274:1 and 265:1 calculated from the particulate data and from the photosynthetic carbon and added (fertilizer) P, respectively, present strong evidence that nutrient limitation was reduced in TA during treatment, but still indicates a high degree of nutrient limitation when compared with the Redfield ratio. Obviously, the phytoplankton community of Sproat Lake is highly efficient at sequestering all available nutrients; and it is nutrient availability which controls photosynthetic rates.

Since allochthonous nutrient supplies to the epilimnion of Sproat Lake are normally so low, requirements of both bacteria and phytoplankton during stratified periods must be met almost entirely from regenerated sources (e.g. zooplankton excretion, microbial loop, littoral zone). It has been well documented that grazing by microflagellates, ciliates, and microzooplankton on free-living bacteria and algal picoplankton plays an important role in nutrient regeneration and dissolved organic carbon (DOC) release in the pelagic zone of both marine and freshwater oligotrophic ecosystems (Goldman and Caron 1985; Sherr et al. 1986; Scavia et al. 1986; Stockner and Porter 1988). In the epilimnion of Sproat Lake in spring, microphytoplankton (mainly diatoms) comprise over 90% of phytoplankton biomass (as volume), and these larger phytoplankters are no doubt responsible for a substantial proportion of the lake's 'new' photosynthesis. However, for the remainder of the growing season heterotrophic and autotrophic pico- and nanoplankton increased in importance, comprising up to 40% of the biomass. Also, our size-fractionated photosynthetic studies show that high metabolic activities occur in the small phytoplankton, with algal picoplankton accounting for an average of 50% of total photosynthesis. Similarly, in oligotrophic Lake Superior, approximately 50% of annual photosynthesis is attributable to cells passing a 3-μm screen (Fahnenstiel et al. 1986). In mesoeutrophic Lake Konstanz, Weisse (1988) has recently shown that algal picoplankton account for only about 15% of total phytoplankton carbon production. These data suggest that in more productive systems where nutrient loads to the lake are sufficient to support 'new' photosynthesis for much of the growing season, algal picoplankton are less important both in terms of their contribution to carbon budgets (photosynthesis) and to DOC and nutrient regeneration. In Sproat Lake, the relative importance of picoplankton did not decrease during fertilized periods, most likely because the very stable epilimnion in Sproat Lake was an unfavorable environment for large celled, fast sinking microphytoplankton. In other lakes we have studied which have more wind-induced vertical mixing, fertilization has resulted in much greater increases in microplankton density (Stockner and Shortreed 1988). Further, although fertilization produced substantial increases in productivity, the lake remained oligotrophic throughout the study. Because of their small size and high efficiency in sequestering nutrients, members of the microbial community have extremely low sinking rates and are a persistent feature of nutrient impoverished ecosystems where 'new' photosynthesis is negligible (Landry et al. 1984; Stockner and Shortreed 1988).

DCM

Various mechanisms have been proposed to explain development and maintenance of DCM in lakes (Fee 1976; Moll and Stoermer 1982; Pick et al. 1984; Fahnenstiel and Scavia 1987). Since the DCM in Sproat Lake developed after the spring epilimnetic chlorophyll maxima and occurred at the bottom of or below the euphotic zone, and since photosynthesis at the DCM was not always detectable, it is evident that in Sproat Lake its development and maintenance are not due exclusively to active photosynthesis at depth. Spring epilimnetic photosynthesis and the onset of stratification convert the surface waters of the lake from a moderately high nutrient-high light environment to a (very) low nutrient-high light environment. Phytoplankton cells (most notably *Rhizosolenia*) unable to compete in these changed conditions sink out of the epilimnion into a moderate nutrient-low light environment, and contribute to both hypolimnetic photosynthesis and to the DCM. Further, substantial hypolimnetic photosynthesis occurs above the DCM, and undoubtedly contributes to its maintenance. This was verified by the continued increases in *Rhizosolenia* numbers at the DCM after it was virtually absent from the epilimnion (Fig. 8). Several investigators (Fee 1976; Moll et al. 1984) have found that substantial photosynthesis occurred at the DCM, and while photosynthesis at the DCM in Sproat Lake was low, it was often detectable. Fee (1976) reported that photosynthesis of hypolimnetic phytoplankton in ELA lakes was inhibited by exposure to the higher light levels in the epilimnion, but in our study increases in light intensity stimulated photosynthesis in DCM phytoplankton, clearly indicating that cells were viable and that photosynthesis at the DCM was light-limited. Maximum light intensities (midday, mid-summer) at the DCM generally ranged from 5–10 $\mu E \cdot m^{-2} \cdot s^{-1}$, which were similar to levels at which photosynthesis in Lake Michigan was found to be primarily light-limited (Fahnenstiel et al. 1984). The viability of cells at the DCM was further verified by the increases in near-surface photosynthetic rates which occurred when fall mixing dispersed the DCM and increased phytoplankton biomass in the upper portion of the water column (Figs. 4, 5). Collectively these data suggest that the DCM in Sproat Lake is maintained by passive processes as well as by active photosynthesis. Hypotheses advanced by several authors (Menzel and Ryther 1960; Steele and Yentsch 1960; Kiefer and Kremer 1981) to explain formation of a DCM in the oligotrophic ocean suggest that nutrient-impoverished phytoplankton produced in shallower waters accumulate at the DCM because of a deceleration in sinking rates in the colder, low light, nutrient-rich waters. This mechanism has been shown to be active in Sproat Lake, and provides a partial explanation of the DCM in our study lake (Jackson et al. 1989). During the second year of fertilization of TA in late June–early July, water transparency and the euphotic depth were reduced due to increased algal biomass in the epilimnion. Concurrent with the reduced light at depth was the reduction of the DCM. After cessation of fertilization in early July and increased water clarity the DCM was restored, providing further evidence of the strong influence of light on the DCM.

Another factor which can result in an overestimation of the importance of the DCM (as determined by chlorophyll or in vivo fluorescence) is an increase in the amount of chlorophyll/cell as a result of decreasing light intensities (Cullen 1982). In Sproat Lake this was difficult to quantify by analysis of phytoplankton density or biomass because of changes in community structure between epilimnetic and DCM populations. However, evidence that this was a contributing factor to the DCM in Sproat Lake is provided by our particulate carbon (PC) analyses. Although the allochthonous contribution to the PC pool is unknown, the very low external loading in Sproat Lake makes it possible to assume that vertical distribution of allochthonous PC is relatively uniform. On almost all sampling dates, ratios of PC/chlorophyll were substantially higher in the epilimnion than in the hypolimnion, suggesting an increase in the amount of chlorophyll/cell below the thermocline, and at least some adaptation to the low light intensities in the hypolimnion.

To conclude, the DCM in Sproat Lake is formed and maintained by processes occurring above it (accumulation of viable phytoplankton cells), by occasional photosynthesis at the DCM, and by an increase in the amount of chlorophyll/cell. Although zooplankton grazing can have a substantial effect on the size and structure of the DCM (Fahnenstiel and Scavia 1987), this is likely not the case in Sproat Lake because of the considerable numbers of juvenile sockeye salmon which spend their first 1–2 yr of life in the lake. Since they are planktivores, they are very dependent on zooplankton production for growth and survival. Juvenile sockeye avoid water temperatures >16°C (Foerster 1968), so for a substantial portion of the year the epilimnion of Sproat Lake is not utilized by sockeye. Further, in most lakes (including Sproat Lake), juvenile sockeye exhibit a diel vertical migration in which they migrate upward at dawn and dusk to depths of between 30 m and the thermocline for active feeding. Consequently, the DCM occurs at depths which have the highest grazing pressure on zooplankton, and therefore low macrozooplankton densities (K. S. Shortreed and J. G. Stockner, unpubl. data).

The general objective of the nutrient additions to Sproat Lake was to increase zooplankton production and consequently benefit juvenile sockeye growth and survival. This technique has been used in a number of other British Columbia lakes and has been highly successful (Hyatt and Stockner 1985; Stockner and Shortreed 1985; Stockner 1987). However, we propose that a number of the limnological features of Sproat Lake may reduce the success of the technique. Zooplankton genera in Sproat Lake (*Daphnia*, *Eubosmina*, and *Diacyclops*) do not exhibit significant diurnal migrations (K. S. Shortreed and J. G. Stockner, unpubl. data), so stimulation of epilimnetic photosynthesis will largely benefit zooplankton residing there. Any benefits to hypolimnetic plankton or fish populations accruing from surface nutrient additions would be dependent on sinking losses from the epilimnetic phyto- and zooplankton communities. Increasing trophy through nutrient additions will eventually reduce hypolimnetic photosynthesis as increasing epilimnetic phytoplankton biomass reduces light penetration and euphotic zone depth (Moll and Stoermer 1982). We suggest that this reduction has a deleterious effect on juvenile sockeye, although it would be offset to some degree by the increased influx of sinking epilimnetic microphytoplankton, zooplankton, and faeces. In our fertilization experiment, the 1985 loading rate stimulated epilimnetic photosynthesis without reducing hypolimnetic phytoplankton biomass. However, the higher loading rate in 1986 increased epilimnetic phytoplankton biomass to such a degree that compensation depths were reduced. Consequently, hypolimnetic biomass and the DCM were reduced, and not restored until after nutrient additions had stopped, and compensation depths increased to pretreatment levels. Obviously, using nutrient additions as a sockeye enhancement technique in lakes with the characteristics of Sproat Lake requires extreme caution to ensure that effects are beneficial to the target organism(s).

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Dynamics of Age and Size Composition in a Population Subject to Size-Selective Mortality: Effects of Phenotypic Variability in Growth

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A stochastic model for the dynamics of age and size distributions in a population subject to size-selective mortality is derived. Growth variability results from both environmental disturbances and intrinsic differences in the expected asymptotic length of the individuals. The selective harvest of larger fish results in a selective removal of intrinsically faster-growing individuals. Estimation trials indicate that sources of growth variability are difficult to identify from standard catch information. The implications of this uncertainty in a yield per recruit analysis are explored, using parameter estimates of Pacific halibut (*Hippoglossus stenolepis*). At moderate fishing levels yield per recruit increased with the amount of intrinsic variability, but the trend reversed at higher fishing rates. Fishing mortality for maximum expected yield per recruit decreased when the contribution of intrinsic differences to growth variability was larger. Mean spawning biomass was relatively insensitive to the level of phenotypic variability when the population was under moderate-to-heavy exploitation. A standard assumption of yield per recruit analysis, namely, that age-specific selectivities and catch weights are constant, independent of the fishing mortality rate, may result in biassed estimates of mean spawning biomass per recruit, and serious overestimation of optimal fishing levels.

Les auteurs obtiennent par dérivation un modèle stochastique de la dynamique des distributions par taille et par âge d'une population soumise à une mortalité en fonction de la taille. La variabilité de la croissance résulte des perturbations environnementales et des différences intrinsèques des longueurs asymptotiques prévues des individus, dont la variabilité est décrite sous forme de probabilité. Ou encore, diverses formes de croissance peuvent être modélisées séparément. La capture sélective de poissons plus gros entraîne une élimination des individus à croissance intrinsèquement plus rapide. Des essais d'estimation ont montré que les sources de la variabilité de la croissance sont difficiles à déterminer à partir des renseignements généraux fournis par les captures. Les répercussions de ces difficultés dans une analyse de production par recrue sont examinées, à partir d'estimations des paramètres du flétant du Pacifique (*Hippoglossus stenolepis*). Pour des niveaux moyens de prélèvement, la production par recrue a augmenté en fonction de la quantité de variabilité intrinsèque, mais la tendance s'est inversée pour des taux de capture plus élevés. La mortalité causée par la pêche pour une production maximale prévue par recrue a diminué lorsque la contribution des différences intrinsèques à la variabilité de la croissance était plus importante. Si l'on suppose que la sélectivité par âge et les poids à la capture sont constants et indépendants du taux de mortalité causé par la pêche, on peut surestimer très gravement les niveaux optimum de prélèvement. La biomasse moyenne par géniteurs, calculée à l'aide d'un modèle déterministe, présentait également un biais.

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Fish population models typically portray growth of individuals by means of a deterministic function that describes changes in mean size with age. Aside from the obvious fact that models which include growth variability are more biologically realistic, inferences and conclusions drawn from stochastic models may differ from those based on deterministic assumptions. Ignoring the fact that individuals in a cohort have different growth histories can induce biases in the estimation of various rate parameters from size-frequency distributions (e.g. Laurec and Mesnil 1987; Hampton and Majkowski 1987a; Rosenberg and Beddington 1987) and from data on growth increments (Sainsbury 1980; Francis 1988). Many life history parameters have been found to scale on body size, especially when growth is indeterminate. This has provided a rationale for the use of body size, either by itself or coupled with age, as a relevant variable in demographic analysis (see Sauer and Slade 1987, for a review). The incorporation of growth variability into demographic models is beneficial not only for modelling growth per se, but also because it can improve the representation of associated processes, such as mortality, fecundity, etc. When mortality is size-selective, as is the case in most fisheries, variability in growth has a direct effect on the dynamics of abundance. As a consequence, the total yield from a given year-class and its reproductive value may be affected by the extent

and pattern of growth variability among the individuals. The effect of size-selective mortality on mean growth rates in the population will also depend on the particular assumptions made about growth variability.

A stochastic model for a size- and age-structured population was developed by Deriso and Parma (1988). Growth and demography in that model are interconnected through size-selective (fishing) mortality. The model is flexible in various ways. A discrete linear growth equation is applied to some normalizing transformation of fish length, and the resulting normal distribution is propagated over time by a recursive update of its parameters. The distribution of size-at-age can assume a variety of shapes depending on the transformation chosen. Gear selectivity can be made a function of size and age, and the effects of a number of fishing gears, each with a different selectivity function, can be incorporated.

Perhaps the most restrictive assumption in that analysis is that variability in growth increments for fish of a given size is all ascribed to stochasticity in the environment. Successive size increments experienced by an individual are independent random variables, with means solely a function of the size of the fish at the beginning of the growth period. Equations used to describe average growth increments as a function of size are identical for all individuals in the population. A more realistic assumption would be that variability of growth increments results from two sources: (1) differences in the intrinsic growth potential of the individuals, and (2) environmental effects. Heterogeneity in growth rate between sexes of other growth morphs could be included as part of (1).

If growth variability results in part from differences intrinsic to the individuals, size-selective harvesting will alter the phenotypic composition among the survivors. Hence, parameter values describing mean growth rate of the individuals in a cohort will change as the cohort ages. Changes in average growth pattern with age, presumably due to size selection, have been reported for several fish populations (e.g. Parker and Larkin 1959; Ricker 1969; Winters 1981; Post and Prankevicius 1987). An assessment of the effect of these changes on expected yield from a cohort, and fishing rates for maximum yield per recruit, has been precluded by the lack of an appropriate model. When males and females exhibit different growth patterns, the selective harvest of larger individuals will skew the sex ratio of the survivors. The analyses of size or age frequency distributions of pooled sexes, based on assuming a one-to-one sex ratio, could bias the estimates of spawning-stock abundance.

In this paper we extend the analysis in Deriso and Parma (1988) to incorporate individual variability in growth potential, and explore the effects of this variability on expected yield and reproductive potential of a cohort. We follow two different approaches. In the first we assume that the population is composed of a continuum of growth phenotypes, each characterized by a specific asymptotic length. Individuals are randomly assigned to a growth phenotype early in their lives. The distribution of expected asymptotic log-lengths for fish of a given cohort is assumed to be normal, with parameters that change over time through the effect of size-selective mortality. The magnitude of the change is a function of fishing intensity. In the second approach we assume that a discrete number of growth morphs can be identified in the population, such as when males and females exhibit different growth patterns. The dynamics of the growth morphs are modelled separately, and so each morph can be characterized by a complete set of distinct parameter values. Size-selective mortality changes the relative abundance of the growth morphs.

The mathematics of the model are developed in sections 1 and 2. Section 3 focusses on the estimation of growth parameters from standard fishery data on length-age distributions in the catch. A yield per recruit analysis based on modelling growth variability as a continuum of growth phenotypes (the first approach) is developed in section 4; the effects of assuming different levels of phenotypic variability on expected yield per recruit and reproductive potential, and on the computation of optimal fishing rates are explored numerically.

Most of the theory derived by Deriso and Parma (1988) applies to the generalized model presented here. In particular, results in that paper referring to survival and abundance of single cohorts, size distribution for aggregated ages, and estimation of model parameters apply with no modifications to the case in which the population is composed of a continuum of growth phenotypes. When, instead, a discrete number of phenotypes is assumed, results in Deriso and Parma (1988) apply to the separate analysis of each growth morph. Combining the dynamics of the different growth morphs into a single model for the cohort requires only a trivial extension of the published analysis. The equations describing growth and survival of a cohort, as derived in Deriso and Parma (1988), are summarized in Table 1. A glossary of parameters and functions is given in Appendix D.

1. Growth Model with Individual Variability

Variability has been incorporated into empirical growth models by making either one of two radically different assumptions: (1) all variability is attributed to environmental disturbances, which independently affect the individuals in the population (as in Cohen and Fishman 1980; Deriso and Parma 1988; Sullivan et al. 1989), or (2) variability is caused by the individuals having intrinsically different growth potentials (as in Sainsbury 1980; Hampton and Majkowski 1987b; Rosenberg and Beddington 1987; Francis 1988; DeAngelis and Huston 1987; Burr 1988). Kirkpatrick (1984) analyzed separately the two types of models, which he referred to as the "variable-growth" model and the "assignment-at-birth" growth model. In the first type, all individuals of a given initial size have a common expected growth trajectory, from which they depart through the effects of some extrinsic random variable. In the second, each individual follows a distinct growth pattern that is completely determined at some initial stage. Growth trajectories are described by simple deterministic functions, the parameters of which vary among the individuals. In some size-structured fishery models (e.g. Schnute 1987; Jones 1981), individuals recruit at some given size (but variable age), after which they all grow according to a common deterministic function. A limitation of this treatment is that, when growth rate decreases with size, variability in size-at-age resulting from prerecruitment processes shrinks as time progresses due to growth compensation. While growth compensation has been documented for some fish species (Ricker 1969), in many cases variance of size increases with age (see examples in Sainsbury 1980).

Here we derive a growth model that incorporates three sources of variability of size-at-age: the environmental and intrinsic sources of growth variability, and, in addition, variability in the initial size distribution. We will loosely use the term phenotypic to refer to the differences in growth rate which

are intrinsic to the individuals, irrespective of whether these differences have a genetic basis or not. We assume that the modelled population is composed of different growth phenotypes, each characterized by a given growth potential, the expression of which is affected by random environmental disturbances. The intrinsic component then corresponds to the "assignment-at-birth" assumption, and the environmental to the "variable-growth" assumption.

Following Deriso and Parma (1988), we use a stochastic difference equation to recursively model the growth of an individual in the population as

$$(1)\quad x_{a+1} = \alpha + \beta x_a + \epsilon_a,$$

where x_a denotes the natural logarithm of length of an individual of age a and ϵ_a is a normal random variable with mean 0 and variance $V_\epsilon(a)$, which represents environmental effects. We assume that environmental disturbances independently affect the individuals in the population. The model is a stochastic version of the Gompertz growth model applied to length. Let $a=0$ be the initial coded age at which we begin modelling individual growth and assume for simplicity that $V_\epsilon(a)$ is constant and independent of age, say equal to V_ϵ. Then, if all the individuals have the same growth potential (i.e. they have same growth parameters, the case considered in Deriso and Parma (1988)), and the initial distribution of log-length in a cohort is normal with mean $E_x(0)$ and variance $V_x(0)$, the distribution of log-length in the cohort after a years is normal with mean and variance given respectively by

$$(2.1)\quad E_x(a) = \frac{\alpha}{1-\beta} + \left[E_x(0) - \frac{\alpha}{1-\beta}\right]\beta^a \text{ and}$$

$$(2.2)\quad V_x(a) = V_x(0)\beta^{2a} + V_\epsilon\left[\frac{1-\beta^{2a}}{1-\beta^2}\right],$$

which follows from applying the recursive equations (e) and (f) in Table 1 (with $\tau=0$) a times. We will further assume that $0<\beta<1$ and $E_x(0)<\alpha/(1-\beta)$, which implies that expected log-length is an increasing function of age with asymptote $E_x(\infty) = \alpha/(1-\beta)$. A nice property of the model above is that the discrete growth equation preserves the normality of the initial size distribution. Thus, a complete description of size distribution at age can be achieved by analytically propagating the mean and variance of size through time. The use of log-length was motivated by the observation that distributions of size-at-age usually show some degree of skewness; any other normalizing transformation could be used instead.

We follow two approaches to incorporate intrinsic differences in growth potential into the model above. In the first (Model I) we assume that the population is composed of a continuum of growth phenotypes; in the second (Model II) we assume that a discrete number of growth morphs exist.

Model I: A Continuum of Growth Phenotypes

In order to provide for intrinsic differences in growth rate and, at the same time, retain a tractable growth model, we postulate that all individual variability in growth potential can be captured in the "α" parameter. Specifically, we assume that individuals in the population are assigned a value of α at some initial stage, which they retain throughout their lives. Equation (1) still describes the growth increments of an individual, but now α has a distinct value which characterizes that individual's intrinsic growth potential. The expected growth trajectory of that individual is then dependent (that is, statistically conditional) on the value of x_0 and α.

In order to characterize the distribution of size-at-age in a cohort, we need to specify initial conditions. We assume that an individual chosen at random from a cohort at coded age 0 will have some pair of values (x_0, α), the distribution of which is bi-variate normal with parameters $E_x(0)$, $V_x(0)$, $E_\alpha(0)$, $V_\alpha(0)$, and $\mathrm{Cov}_{x,\alpha}(0)$. The latter three symbols denote the mean and variance of α, and the initial covariance between α and x. This is a natural extension of the assumptions made before for the case of $V_\alpha(0)=0$. The assumption that α is normally distributed with parameters $E_\alpha(0)$ and $V_\alpha(0)$ implies that the expected asymptotic log-length of the individuals in the cohort is normally distributed with mean and variance given by

$$\text{Mean} = \frac{E_\alpha(0)}{1-\beta} \text{ and}$$

$$\text{Variance} = \frac{V_\alpha(0)}{(1-\beta)^2}.$$

It is important to note, however, that the asymptotic ($a\to\infty$) mean of the distribution of log-length in a cohort, $E_x(\infty)$, coincides with the expected asymptotic log-length as given in the formula above only in the absence of size-specific mortality. The condition that mortality rates are free from size dependence is necessary to assure that the distribution of α remains unchanged throughout the lifetime of the cohort. We later incorporate the effects of size-selective mortality into the model and show that the distribution of α, and in turn that of $E_x(\infty)$, change in a predictable way as a function of the mortality parameters.

One subtlety of the model is that individual differences in growth potential (as captured in the α parameter) may be already apparent during juvenile stages, long before animals recruit into the fishery. In other words, animals can be "assigned" a particular value of α at an age younger than coded age 0. If this were the case, the larger individuals at age 0 would be on average those with larger α values, and so the initial covariance between x and α would be positive. Assuming instead that $\mathrm{Cov}_{x,\alpha}(0)=0$ implies that individuals are "assigned" a particular value of α right before they recruit, and that the assignment is random. Although x and α may be initially independent, a positive covariance builds up through the growth process. In Appendix A, we present a formal derivation of this intuitively obvious result and show that the bi-variate normal property of the initial distribution of (x,α) is retained through the growth process. We first present growth equations for a cohort in which mortality is free of size dependence. Assuming that the environmental disturbance ϵ_a that affects each individual's growth increment is independent of x_a and α, the recursive equations for updating the parameters of the bi-variate normal distribution of (x,α) are

$$(3.1)\quad E_x(a+1) = E_\alpha(a) + \beta E_x(a)$$

$$(3.2)\quad V_x(a+1) = V_\alpha(a) + \beta^2 V_x(a) + 2\beta\mathrm{Cov}_{x,\alpha}(a) + V_\epsilon(a)$$

$$(3.3)\quad \mathrm{Cov}_{x,\alpha}(a+1) = V_\alpha(a) + \beta\mathrm{Cov}_{x,\alpha}(a),$$

where the mean and variance of α in the absence of size-specific mortality are in fact equal to their initial values, that is $E_\alpha(a) = E_\alpha(0)$ and $V_\alpha(a) = V_\alpha(0)$.

In order to derive age-dependent trajectories for the parameters above we need to specify how the variance of environmental disturbances, $V_\epsilon(a)$, changes with age. The simplest assumption is to make $V_\epsilon(a) = V_\epsilon$, a constant. As discussed in

Deriso and Parma (1988), it seems more reasonable to assume that the greater the expected growth increment, the greater its variability. $V_\epsilon(a)$ can be made proportional to the age-specific expected growth increment this is

$$V_\epsilon(a) \propto [E_\alpha(a) + (\beta - 1)E_x(a)].$$

Substituting equation (3.1) for $E_x(a)$ we can see that this is equivalent to assuming that

$$V_\epsilon(a) = V_\epsilon(0)\beta^a.$$

Thus, if growth is asymptotic (i.e. $\beta<1$), the environmentally induced variability of growth increments decreases exponentially with age. This diminishes the chance that individual increments in x be negative, since their variance tends to zero as $a\rightarrow\infty$ and $E_x(a)$ approaches its asymptotic value.

In the first case, where $V_\epsilon(a) = V_\epsilon$, the parameters of the binormal distribution of (x,α) are given by

$$(4.1)\quad E_x(a) = \frac{E_\alpha(0)}{1-\beta} + \left[E_x(0) - \frac{E_\alpha(0)}{1-\beta}\right]\beta^a,$$

$$(4.2)\quad V_x(a) = V_x(0)\beta^{2a} + V_\epsilon\left[\frac{1-\beta^{2a}}{1-\beta^2}\right] + V_\alpha(0)\left[\frac{1-\beta^a}{1-\beta}\right]^2 + 2\mathrm{Cov}_{x,\alpha}(0)\beta^a\left[\frac{1-\beta^a}{1-\beta}\right] \text{ and}$$

$$(4.3)\quad \mathrm{Cov}_{x,\alpha}(a) = V_\alpha(0)\left[\frac{1-\beta^a}{1-\beta}\right] + \mathrm{Cov}_{x,\alpha}(0)\beta^a,$$

as shown in Appendix A. Notice that if $V_\alpha(0)=0$ (and, consequently, $\mathrm{Cov}_{x,\alpha}(0)=0$) the above equations reduce to equations (2). When the initial covariance is zero but $V_\alpha(0)$ is positive, the three leading terms in equation (4.2) correspond to the three variability components mentioned earlier: the environmental, the intrinsic, and the variability resulting from the initial distribution of x. Since $0<\beta<1$, the latter component plays a dominant role when animals are young and it gradually vanishes as the cohort ages. If $V_x(0)$, variance of the initial distribution, were assumed to be the only source of variability, then variance of log-length-at-age would decrease asymptotically to zero. In general, though, as the cohort becomes older $V_x(a)$ converges to the following positive value, which reflects environmental and intrinsic variability:

$$V_x(\infty) = \frac{1}{1-\beta}\left[\frac{V_\epsilon}{1+\beta} + \frac{V_\alpha(0)}{1-\beta}\right].$$

In the second case, where $V_\epsilon(a)$ is proportional to the age-specific expected growth increment, the age-dependent trajectory of the variance parameter is as before except for the second term in (4.2), the environmental component, which is replaced by

$$V_\epsilon(0)\beta^{a-1}\left[\frac{1-\beta^a}{1-\beta}\right].$$

This expression follows after applying the recursive equation (3.2) a times, where $\epsilon_a \sim N(0, V_\epsilon(0)\beta^a)$ and initial conditions are as before. Under this assumption about $V_\epsilon(a)$, then, the variance component induced by the environment is no longer a monotonically increasing function of age. Instead, it first increases while $\beta^a > 1/2$ and then it decreases to zero. As $E_x(a)$ converges to its asymptotic value, the phenotypic component plays an increasingly dominant role, and $V_x(a)$ converges to

$$(5)\quad V_x(\infty) = \frac{V_\alpha(0)}{(1-\beta)^2},$$

the variance of the population parameter corresponding to asymptotic log-length. Notice that terms involving $V_\epsilon(0)$ and $\mathrm{Cov}_{x,\alpha}(0)$ in the full expression for $V_x(a)$ can be combined so that

$$(6)\quad V_x(a) = V_x(0)\beta^{2a} + (V_\epsilon(0) + 2\beta\mathrm{Cov}_{x,\alpha}(0))\beta^{a-1} \times \left[\frac{1-\beta^a}{1-\beta}\right] + V_\alpha(0)\left[\frac{1-\beta^a}{1-\beta}\right]^2.$$

This indicates that the effect of $V_\epsilon(0)$ and $\mathrm{Cov}_{x,\alpha}(0)$ on $V_x(a)$ are completely confounded.

Model II: Discrete Growth Phenotypes

An alternative approach to incorporate individual variability in growth potential is to assume that the population contains a discrete number of growth morphs represented in some variable proportion. This would be the natural way to model populations in which males and females have different growth patterns, such as was done by Cohen and Fishman (1980). We could assume that between-morphs heterogeneity is the sole source of phenotypic variability, or we could in fact combine the two approaches by including within-morph phenotypic variability. For simplicity, consider the case where only between-sexes differences are incorporated, and each sex has a distinct set of growth parameters. The equations derived above for the case of $V_\alpha(a)=0$ can be used to separately represent growth for each sex. The distribution of log-length for a cohort is no longer normal but a mixture of normal components. The mean and variance of the combined distribution results from weighing the sex-specific first and second noncentral moments by the relative abundances of the two sexes (see Appendix C for more details).

2. Growth and Abundance under Size-Selective Mortality

In order to incorporate the effects of size-selective mortality, we make assumptions similar to those in Deriso and Parma (1988). These are:

(1) Year t is divided into two parts, with fishing occurring over the time interval $[t, t+\tau]$, and growth and natural mortality over $[t+\tau, t+1]$. The fishing season is assumed to be arbitrarily short, so that growth and natural mortality over the season can be neglected.

(2) The size-specific risk of fishing mortality $F(t, x)$ is constant over $[t, t+\tau]$, and is separable into a product of a full-recruitment fishing mortality rate and a factor $S(x)$ representing gear selectivity for fish of size x, so that $\int_t^{t+\tau} F(z,x)dz = F_t S(x)$. The probability of capture for an individual of size x in year t is then given by

$$pr(\text{fish captured}|x) = 1 - e^{-F_t S(x)},$$

where $pr(\cdot|\cdot\cdot)$ is the probability that event $(\cdot)$ occurs given $(\cdot\cdot)$. Size-selectivity is approximated by a series of second order polynomials, where each polynomial "best fits" an assumed selectivity function (such as a logistic curve) over the range of sizes of a given age class. The size-dependent probability that an individual of age a survives the harvest season in year t is then approximated by

$$pr(\text{fish survives}|x,a,t) = e^{-F_t(b_0 + b_1 x + b_2 x^2)},$$

where b_0, b_1, and b_2 are age-specific coefficients which can be obtained by one of the procedures discussed in Deriso and Parma (1988). A numerical analysis of the performance of those procedures can be found in Parma (1989).

(3) The risk of natural mortality $M(t)$ is constant over $[t+\tau, t+1]$ and independent of size.

In the previous section we showed that if the growth parameter α is a random variable and a particular value of α is independently and randomly assigned to each individual at some initial stage, a positive correlation between fish size and α builds up through the growth process. As a consequence, the selective harvest of larger fish results in a selective removal of intrinsically faster-growing individuals. When mortality is size-selective, therefore, the probability density function of α changes over the lifetime of the cohort. In what follows we will emphasize the most common case in which the probability of capture increases with fish size. Note, however, that the theory is in fact valid for any arbitrary function $S(x)$.

Suppose that the joint density of (x,α) for fish of age a prior to the fishing season in year t is, as before, bi-variate normal with parameters $E_x(a,t)$, $V_x(a,t)$, $E_\alpha(a,t)$, $V_\alpha(a,t)$, and $\mathrm{Cov}_{x,\alpha}(a,t)$. Notice that the notation here is as in the previous section, except for the incorporation of the index for year t. In what follows, we will omit the time index whenever we refer to individual cohorts subject to a constant fishing rate. In order to see how the pdf of (x, α) is affected by size-selective mortality, we first write the joint density of (x, α) following the fishing season as:

$$(7)\quad f(x,\alpha|\text{fish survives}) = f(\alpha|x, \text{fish survives}) f(x|\text{fish survives}),$$

where $f(\cdot|\cdot\cdot)$ denotes the conditional pdf of $(\cdot)$ given $(\cdot\cdot)$. The pdf of α conditional on the size of the fish following the fishing season can be written using Bayes theorem as

$$f(\alpha|x,\text{fish survives}) = \frac{pr(\text{fish survives}|\alpha,x) f(\alpha|x)}{pr(\text{fish survives}|x)}.$$

As the probability of a fish surviving from fishing depends on its size alond, i.e. it is independent of the value of α, the probabilities in the numerator and denominator are equal and then

$$(8)\quad f(\alpha|x,\text{fish survives}) = f(\alpha|x).$$

This proves the intuitively appealing result that the pdf of α conditional on size for fish that survived the harvest is the same as the pdf of α given size prior to the fishing season. In other words, the conditional distribution of the growth parameter α given fish size is not affected by size-selective-mortality over a single fishing season. This result is the key that allows us to update the parameters of the marginal (unconditional) distribution of α through each of the successive fishing seasons experienced by a cohort.

The second density on the right side of equation (7) is the pdf of log-length of a cohort after the fishing season. As shown by Deriso and Parma (1988), this pdf is approximately normal with mean $E_x(a+\tau, t+\tau)$ and variance $V_x(a+\tau, t+\tau)$, given in Table 1. This results from having approximated $S(x)$ by a quadratic function. As the conditional pdf of α given fish size is not altered over the fishing season and the pdf of x remains normal, the bi-variate normal distribution of (x, α) is propagated. In Appendix B, we show that the mean and variance of α, and the covariance of x and α can be updated recursively as follows:

$$(9.1)\quad E_\alpha(a+\tau,t+\tau) = E_\alpha(a,t) + \frac{\mathrm{Cov}_{x,\alpha}(a,t)}{V_x(a,t)}\,(E_x(a+\tau,t+\tau) - E_x(a,t))$$

$$(9.2)\quad V_\alpha(a+\tau,t+\tau) = V_\alpha(a,t) + \left[\frac{\mathrm{Cov}_{x,\alpha}(a,t)}{V_x(a,t)}\right]^2 \times (V_x(a+\tau,t+\tau) - V_x(a,t))$$

$$(9.3)\quad \mathrm{Cov}_{x,\alpha}(a+\tau,t+\tau) = \frac{\mathrm{Cov}_{x,\alpha}(a,t)}{V_x(a,t)}\, V_x(a+\tau,t+\tau).$$

These three parameters, together with $E_x(a+\tau, t+\tau)$ and $V_x(a+\tau, t+\tau)$ in Table 1, completely characterize the bi-variate normal distribution of (x, α) for fish of age a following the harvest season. The shifts in the mean and variance of α resulting from size-selective harvest are respectively proportional to the corresponding shifts in the mean and variance of log-length of fish in the cohort. Also, the larger the covariance between x and α, the stronger the effect of a size-selective mortality on the marginal distribution of α and, consequently, on the mean growth rate of the individuals that survive the harvest.

As natural mortality is assumed independent of fish size, equation (3) (with a on the right hand side replaced by $(a+\tau, t+\tau)$) can be applied to the recursive equations just derived, and to those for $E_x(a+\tau, t+\tau)$ and $V_x(a+\tau, t+\tau)$ in Table 1, to obtain the parameters of the joint distribution of (x, α) for the same cohort at the beginning of year $t+1$ following the growth period. This gives

$$E_x(a+1,t+1) = E_\alpha(a,t) - F_t \mathrm{Cov}_{x,\alpha}(a,t)\,\frac{2b_2E_x(a,t)+b_1}{2b_2F_tV_x(a,t)+1} + \beta\left[\frac{E_x(a,t) - b_1F_tV_x(a,t)}{2b_2F_tV_x(a,t)+1}\right]$$

$$V_x(a+1,t+1) = V_\alpha(a,t) + V_\epsilon(a) + \frac{\beta^2V_x(a,t) + 2\beta\mathrm{Cov}_{x,\alpha}(a,t) - 2b_2F_t\mathrm{Cov}_{x,\alpha}(a,t)^2}{2b_2F_tV_x(a,t)+1}$$

$$E_\alpha(a+1,t+1) = E_\alpha(a,t) - F_t\mathrm{Cov}_{x,\alpha}(a,t)\left[\frac{2b_2E_x(a,t)+b_1}{2b_2F_tV_x(a,t)+1}\right]$$

$$V_\alpha(a+1,t+1) = V_\alpha(a,t) - 2b_2F_t\left[\frac{\mathrm{Cov}_{x,\alpha}(a,t)^2}{2b_2V_x(a,t)+1}\right]$$

$$\mathrm{Cov}_{x,\alpha}(a+1,t+1) = V_\alpha(a,t) + \mathrm{Cov}_{x,\alpha}(a,t) \times \left[\frac{\beta - 2b_2F_t\mathrm{Cov}_{x,\alpha}(a,t)}{2b_2F_tV_x(a,t)+1}\right].$$

If x and α are initially independent, so that $\mathrm{Cov}_{x,\alpha}(0, t) = 0$, the first size-selective harvest will not affect the marginal distribution of α. After one growing season, however, a positive covariance between α and x ($\mathrm{Cov}_{x,\alpha}(1, t+1) = V_\alpha(0, t)$) will build up, and hence size-selective harvest will have an effect on the pdf of α. The larger the initial variance of α, the stronger the effect of a size-selective fishery on the growth rate of a cohort. For the limiting case where $V_\alpha(0,t) = 0$, the equations derived here correspond to those in Table 1.

Figure 1 illustrates how the median of length (given by $\exp\{E_x(a)\}$) and the variance of x can be affected by fishing, for two levels of phenotypic variability, given in terms of $CV(L_\infty)$, the coefficient of variation of the expected asymptotic length of a year-class,

TABLE 1. Equations for growth and survival of a cohort, from Deriso and Parma (1988). Size-selectivity is approximated by a series of quadratic functions (with coefficients b_0, b_1, and b_2), one for each age. Fish size x is the logarithm of length of a fish. $E_x(a)$ and $V_x(a)$ are the mean and variance of x, $p(a)e^{-M}$ is the probability of annual survival, and $l(a)$ is the cumulative probability of survival from reference age 0 to age a. Size-selective fishing takes place from time t to time $t+\tau$, while growth and natural mortality take place from $t+\tau$ to $t+1$; τ is arbitrarily small. Year indices have been dropped from all notation in the table.

	Time interval	
	From time t to $t+\tau$	From $t+\tau$ to $t+1$
(a)	$E_x(a+\tau) = \dfrac{E_x(a) - b_1 F V_x(a)}{2b_2 F V_x(a) + 1}$	(e) $E_x(a+1) = \alpha + \beta E_x(a+\tau)$
(b)	$V_x(a+\tau) = \dfrac{V_x(a)}{2b_2 F V_x(a) + 1}$	(f) $V_x(a+1) = \beta^2 V_x(a+\tau) + V_\epsilon$
(c)	$p(a)e^{-M} = \dfrac{1}{\sqrt{2b_2 F V_x(a) + 1}} \cdot \exp\left[-M - Fb_0 - F\left(\dfrac{b_2 E_x(a)^2 + b_1 E_x(a) - b^2 V_x(a) F/2}{2b_2 F V_x(a) + 1}\right)\right]$	
(d)	$l(a) = e^{-Ma} \prod_{j=0}^{a-1} p(j)$	

(10) $CV(L_\infty) = \sqrt{\exp\{V_x(\infty)\} - 1}$.

In one case there is no variability in the asymptotic length, and in the other $CV(L_\infty)$ equals 25%. Parameter values used to construct the figures in the latter case were estimated using Pacific halibut (*Hippoglossus stenolepis*) catch data, as explained later. The trajectories of median length-at-age for a constant fishing mortality $F = 0.3$ generated with the two sets of parameters are similar over the range of ages that form the bulk of the catch in halibut (ages 6 to 16), and they increasingly depart at older ages. Size-selective mortality depresses growth even when all the individuals have same growth potential (solid line), and so both curves are below the trajectory generated in the absence of fishing. The effect of $CV(L_\infty)$ on the progession of $V_x(a)$ (Fig. 1b) is more marked in old ages; patterns are again similar around ages that are well represented in the catches. When $CV(L_\infty) = 25\%$, $V_x(a)$ is a monotonically increasing function of age. In contrast, when there is no phenotypic variability, $V_x(a)$ has a maximum at an intermediate age and decreases thereafter. This reversal occurs when the reduction in $V_x(a)$ due to growth compensation (that is, the convergence of length to asymptotic length) exceeds the increase caused by environmental effects. The effect of fishing is initially to reduce $V_x(a)$,but the trend reverses at older ages, where the size-selectivity curve is concave ($b_2 < 0$ in the quadratic approximation; see equation (b) in Table 1). The coefficient of variation of length is a monotonic function of $V_x(a)$ and so it follows similar trends. In contrast, the trajectory of the variance of length was only slightly affected by the level of phenotypic variability assumed. This is because the effects of shifts in the mean and variance of x on the variance of length-at-age balanced.

Technical details and rationale for values used to construct Fig. 1 are given next. Parameter values are maximum likelihood estimates obtained for Pacific halibut of British Columbia and Washington (International Pacific Halibut Commission (IPHC), regulatory area 2AB). The use of these parameter values is only for illustration, and so we will not describe the estimation procedure in detail. Likelihood equations were developed in Deriso and Parma (1988), and they are summarily described later in section 3. Initial covariance $\mathrm{Cov}_{x,\alpha}(0)$ was set equal to $V_\alpha(0)(1-\beta^6)/(1-\beta)$, where 6 is the true age for coded age $a = 0$. In other words, we assumed random assignments of α to individuals at birth, and used equation (4.3) to give the covariance at true age 6. The level of phenotypic variability corresponding to these parameters can be indicated by noting that when $CV(L_\infty) = 0.25$, in the absence of size-selective mortality, 40% of the variance of x at coded age $a = 6$ (approximately the mean age in halibut catch) is contributed by $V_\alpha(0)$ and $\mathrm{Cov}_{x,\alpha}(0)$. For the case of $CV(L_\infty) = 0$, the same set of parameter values was used except that $V_\epsilon(0)$ was adjusted so that the variance of x at coded age 6 matched that where $CV(L_\infty) = 0.25$ and, of course, $V_\alpha(0)$ was set to zero.

Interestingly, while phenotypic variability may have only a minor effect on the median of length-at-age, the effects may be important when mean growth increments as a function of initial length and age are analyzed. Figure 2 shows, for the same parameter values with $CV(L_\infty) = 25\%$, how the median of asymptotic length increases with initial size for animals of three consecutive ages, when a fishing rate of $F = 0.3$ has been applied. This median is given by $\exp\{E_{\alpha|x}(a)/(1-\beta)\}$, where $E_{\alpha|x}(a)$ denotes the expected value of α conditional on x, for individuals of age a. A 34% increse in asymptotic length is observed for fish of age 8 over a range of sizes corresponding to the 16 and 84% quantiles of the size distribution. The wide bars in the figure mark the median lengths for each age, and the narrow lines the 84 and 16% quantiles for ages 7 and 9, respectively. Older ages have overall lower asymptotic lengths due to size-selective mortality. These effects, if unaccounted, may bias the estimates of mean growth parameters for the population obtained from tag-recovery data, even if the age of the animals is known. One subtlety of the growth model is that, even in the absence of size-selective mortality, expected growth increments depend jointly on initial fish size and age. This age-dependence is induced by the variability of the α parameter: although the mean of α is constant for all ages (when mortality is independent of size), the conditional mean $E_{\alpha|x}(a)$ depends on the other parameters of the joint distribution of (x, α). These parameters are all functions of age. Thus, a fish of age 8 and size equal to the mean for that age, $E_x(8)$, will have a slower

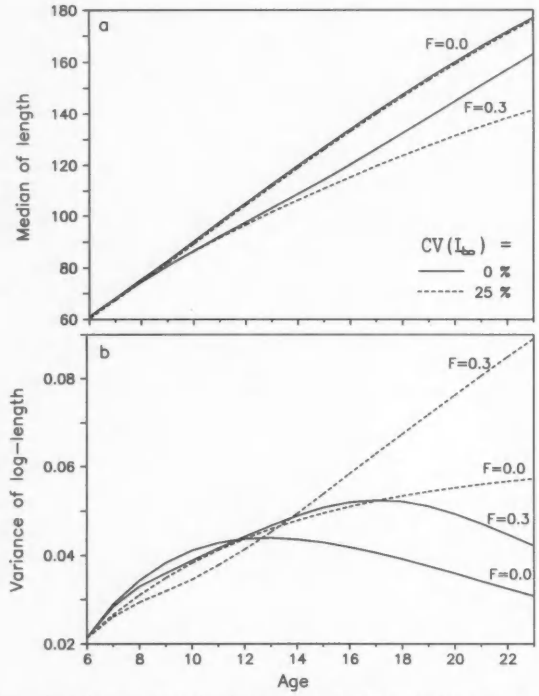

FIG. 1. Effects of size-selective harvest on the distribution of size-at-age when all individuals have same growth potential (coefficient of variation of asymptotic length $CV(L_\infty) = 0$), and when $CV(L_\infty) = 25\%$. (a) Trajectories of median length; (b) trajectories of variance of log-length. F is full-recruitment fishing mortality. Parameter values for $CV(L_\infty) = 25\%$ are: $E_\alpha(0) = 0.41898$, $\beta = 0.92461$, $V_\alpha(0) = 0.000353$, $E_x(0) = 4.3048$, and $V_x(0) = 0.02138$; $V_\epsilon(a,t)$ was proportional to expected growth increment with proportionality constant $V_U = 0.04305$; gear selectivity was a logistic function of length with asymptote equal to 1, length at the inflection point equal to 85.22 cm, and slope at the inflection point $r = 0.05515$.

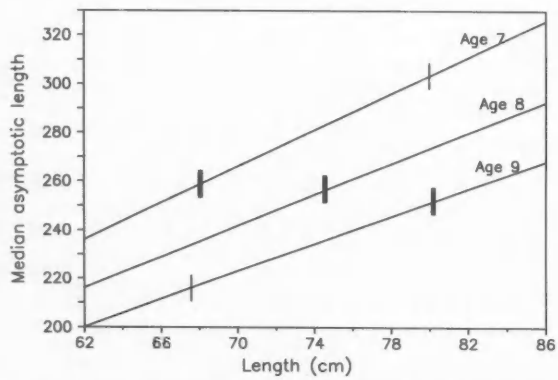

FIG. 2. Effects of size-selective fishing on the median of the asymptotic length conditional on fish size for three consecutive ages. Wide bars mark the median lengths for each age, and narrow lines the 84 and 16% quantiles for ages 7 and 9, respectively. Parameters are the same ones used in Fig. 1, with coefficient of variation of asymptotic length equal to 0.25 and full-recruitment fishing mortality $F = 0.3$.

growth rate than a fish of the same size but of age 7 or younger. This "sorting" of the values of the growth parameters according to the length of the individuals was discussed by Sainsbury (1980), who acknowledged that the assumption in his estimation method that distributions of parameter values are not altered conditional on age or initial length could cause serious problems.

In the preceding analysis we have built the effect of phenotypic variability into the dynamic equations describing how the (approximate) distribution of size-at-age propagates through time. In doing so we have retained the basic property of the model in Deriso and Parma (1988), namely, that the distribution of log-length of individuals in a cohort is approximated by a normal distribution, whose progression through time can be succinctly described by a recursive update of the parameters $E_x(a,t)$ and $V_x(a,t)$. Now, since survival is strictly a size-dependent process, the dynamics of abundance can be modelled in exactly the same way as was done under the assumption of $V_\alpha(a,t) = 0$. Let $\varphi(x|a,t)$ denote the marginal (integrated across α) normal pdf of log-length of individuals of age a before the fishing season of year t. Then the probability $p(a,t)$ that a randomly chosen animal of age a avoids capture in year t is obtained by integrating the joint probability of surviving the harvest and being of log-length x across the range of possible values of x; this is

$$p(a,t) = \int_{-\infty}^{\infty} e^{-F_t(b_0 + b_1 x + b_2 x^2)} \varphi(x|a,t)dx,$$

which is given by equation (c) in Table 1. This probability is conditional on the parameters of $\varphi(x|a,t)$, which in turn depend on the level of phenotypic variability. The indirect effect of changing the relative contribution of intrinsic and extrinsic sources of growth variability on the survival dynamics was minuscule when the two sets of parameter values used to construct Fig. 1 were contrasted.

The cumulative probability that a fish of age zero survives to age a, $l(a,t)$, as given by equation (d) in Table 1, is also valid when $V_\alpha > 0$. In addition, the analysis presented in Deriso and Parma (1988) concerning the abundance and size/age distributions in the catch apply without modifications to the generalized model presented here. We summarize some results from that analysis that we will use later in the estimation section:

1) Abundance of a cohort in year t is binomially distributed with mean and variance

$$E_N(a,t) = R_{t-a} l(a,t) \quad \text{and}$$
$$V_N(a,t) = R_{t-a} l(a,t)[1 - l(a,t)],$$

where R_{t-a} denotes the abundance of the cohort at coded age $a = 0$, and $l(a,t)$ is the cumulative survival from age 0 to age a.

2) The distribution of log-length x in the catch of year t for individuals of age a is given by

$$f^c(x|a,t) = \frac{(1 - e^{-F_t S(x)})\varphi(x|a,t)}{1 - p(a,t)},$$

where $p(a,t)$ is the probability that a fish of age a avoids capture in year t, $\varphi(x|a,t)$ is a normal pdf with parameters $E_x(a,t)$ and $V_x(a,t)$, and $S(x)$ is the gear selectivity for individuals of log-length x.

3) The distribution of log-length in the catch of year t is a mixture of the age specific components:

$$f^c(x|t) = \sum_{a=0}^{A} f^c(x|a,t)P^c_{a,t} ,$$

where $P^c_{a,t}$ is the probability that an animal selected at random in the catch is of age a, and A is the maximum age in the catch. That probability is equal to the expected value of the ratio of the number of individuals of age a in the catch and the total catch in numbers. As shown in Deriso and Parma (1988), the value of $P^c_{a,t}$ can be approximated by the delta method as

$$P^c_{a,t} = \frac{E_N(a,t)(1-p(a,t))}{\sum_{i=0}^{A} E_N(i,t)(1-p(i,t))} .$$

4) The expected value and variance of the catch in numbers in year t are given by

$$E_C(t) = \sum_{a=0}^{A} [E_N(a,t)(1-p(a,t))] \text{ and}$$

$$(11) \quad V_C(t) = \sum_{a=0}^{A} [E_N(a,t)(1-p(a,t))p(a,t) + [1-p(a,t)]^2 V_N(a,t)].$$

Expected values and variance for the catch in biomass are also provided in Deriso and Parma (1988).

The preceding equations are in fact approximations, since an approximated selectivity function is used to maintain a normal distribution for log-length-at-age for all ages.

When phenotypic variability is incorporated as a discrete number of growth phenotypes (Model II), each characterized by a distinct set of parameter values, the equations above can be used to represent separately the dynamics of each morph. Size-selective harvest in that case alters the relative abundance of the growth morphs. Suppose for example that there are only two growth morphs corresponding to males (m) and females (f), which prior to the harvest have size distributions $\varphi(x|a,t,m)$ and $\varphi(x|a,t,f)$ and relative abundances $P_m(a,t)$ and $P_f(a,t)$. The probability that a fish of age a chosen at random after the harvest is of sex s will be given by

$$P_s(a+\tau,t+\tau) = \frac{p(a,t,s)P_s(a,t)}{p(a,t,m)P_m(a,t) + p(a,t,f)P_f(a,t)} ,$$

where $p(a,t,s)$ is the probability that an animal of age a and sex s survives the harvest in year t. The dynamics of the separate models can be simply combined to give the population parameters. In Appendix C we show how to modify the estimation theory developed in Deriso and Parma (1988) to incorporate the existence of separate growth morphs.

3. Sources of Growth Variability are Difficult to Estimate from Catch Data

The standard catch information commonly available in many fisheries consists of a time series of yearly estimates of total catch in biomass, size frequency distributions of the catches, and age-length keys. Judging from the illustrations presented earlier, one can expect that these data contain very little information about the relative contribution of environmental and intrinsic factors to growth variability: changing the relative contribution of the two sources had only a minor effect on the mean and variance of size-at-age, except for the older ages, which are poorly represented in the catches. In fact, when parameter values used to construct Fig. 1 were estimated from Pacific halibut catch data (regulatory area 2AB), we found the likelihood surface to be very flat for a range of values of $CV(L_\infty)$ from zero up to 30%. Values of $CV(L_\infty)$ estimated for other management regions were close to 15%.

In order to better illustrate the problem of identifiability of growth parameters we conducted a number of estimation trials using simulated catch data. The use of artificial data allowed us to specifically focus on the estimation of growth parameters, while holding the rest of the parameters in the model at their known true values. Parameter values used in the numerical exercise are the same Pacific halibut estimates used in the illustrations earlier. In what follows we describe the procedures used for generating the data and estimating model parameters, and the results from the estimation trials.

Maximum Likelihood Estimation

We will assume that the following pieces of data are available for T years: (1) frequency distribution of length for a random sample of the catch, (2) frequency of age-length categories from a subsample of the sample in (1), and (3) total catch in numbers, C_t. Likelihood equations for the case $V_\alpha = 0$ were developed by Deriso and Parma (1988) and they apply without modifications to the case of $V_\alpha > 0$. The log-likelihood for the observations made in each year t has three components, here denoted as Λ^1_t, Λ^2_t, and Λ^3_t, one for each type of observations above. If L_l is the lower extreme of the grid in the size frequency distribution, NL the number of length categories of width ΔL, and n_i the number of animals in the first random sample (which were not aged) that fell in the i-th length category, the logarithm of the first likelihood component up to additive constants can be approximated by

$$\Lambda^1_t = \sum_{i=1}^{NL} n_i \ln(f^c(x_i|t)),$$

where $x_i = \frac{1}{2}[\ln(L_l + (i-1)\Delta L) + \ln(L_l + i\Delta L)]$ is log-length at the mid point of the i-th interval. The approximation consists in using $f^c(x|t)$ at the mid point of the interval instead of computing the area under f^c bounded by the lower and upper x values of the i-th interval. Likewise, the log-likelihood component for the age-length observations can be approximated by

$$\Lambda^2_t = \sum_{i=1}^{NL} \sum_{a=0}^{A} n_{i,a} \ln(f^c(x_i|a,t)P^c_{a,t}),$$

where $n_{i,a}$ is the number of animals of age a observed in the i-th length category. For the third likelihood component, we approximated the probability distribution of catch in numbers, C_t, by a normal with mean $E_C(t)$ and variance $V_C(t)$. Thus,

$$\Lambda^3_t = \frac{-(C_t - E_C(t))^2}{2V_C(t)} - \frac{1}{2}\ln(V_C(t)).$$

In the derivations presented by Deriso and Parma (1988) catch in biomass instead of in numbers was assumed to be known, and a normal approximation was used to construct the likelihood. This motivated the use of the normal approximation here in place of the binomial distribution. The estimation scheme developed for catch in biomass simplifies to the one used here when mean weight of the animals in the catch is assumed to be known. Parameter estimates can be obtained by maximizing

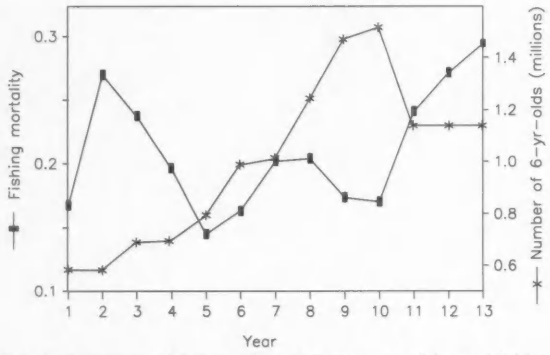

FIG. 3. Sequences of full-recruitment fishing mortalities and initial abundances used to simulate artificial catch data.

$$\Lambda = \sum_{t=1}^{T} [\Lambda_t^1 + \Lambda_t^2 + \Lambda_t^3],$$

where T is the number of years for which catch observations are available.

Data Simulation and Numerical Scheme

Artificial catch data were generated using parameter values estimated for Pacific halibut. Growth parameters in the dynamic equations are: β, the parameters describing the initial bi-variate normal distributions of (x, α) for the $T + A$ cohorts that pass through the fishery over the T years, and the parameter(s) controlling the variability of environmental disturbances. Parameters for the initial distributions are: $E_\alpha(a,t)$, $V_\alpha(a,t)$, $E_x(a,t)$, $V_x(a,t)$, and $\mathrm{Cov}_{x,\alpha}(a,t)$, for $a = 0$ and $t = 1, \cdots, T$, and a similar set for $t = 1$ and $a = 1, \cdots, A$. In order to reduce the number of parameters to be estimated, we made a number of assumptions both when simulating catch data and in the estimation. These are:

1) all cohorts recruiting into the fishery over the T-year period have same initial distributions of (x,α). Under this assumption $E_x(0,t) = E_x(0)$, $V_x(0,t) = V_x(0)$, $E_\alpha(0,t) = E_\alpha(0)$, $V_\alpha(0,t) = V_\alpha(0)$, and $\mathrm{Cov}_{x,\alpha}(0,t) = \mathrm{Cov}_{x,\alpha}(0)$ for $t = 1, \cdots, T$;
2) the mean and variance of log-length for the cohorts present in the catch in the first year of data correspond to the growth trajectory of a synthetic cohort under constant fishing mortality $F = F_{IC}$, where IC stands for initial conditions;
3) initial covariance is equal to $V_\alpha(0)[(1-\beta^6)/(1-\beta)]$, where 6 is the true age of youngest recruits, which corresponds to coded age $a = 0$;
4) variability of individual growth increments induced by the environment is proportional to the age-specific expected increment, such that

$$V_\epsilon(a,t) = V_U[E_x(a+1, t+1) - E_x(a+\tau, t+\tau)],$$

where V_U is constant.

The number of growth parameters was thus reduced to seven, namely, β, $E_\alpha(0)$, $V_\alpha(0)$, $E_x(0)$, $V_x(0)$, V_U and F_{IC}.

Catch data were generated by assuming that length and age-length frequency distributions, and total catch in numbers were exactly as predicted by the model. This is like assuming that initial cohort abundances are sufficiently large, so that the distributions of age and length in the catch, and survival fractions converge to those predicted. In addition, sampling errors were ignored. The effect of these assumptions is to maximize the information content of the data for the given set of parameter values used in the simulation. Growth parameters were: $E_\alpha(0) = 0.41898$, $\beta = 0.92461$, $V_\alpha(0) = 0.000353$, $E_x(0) = 4.3048$, $V_x(0) = 0.02138$, and $V_U = 0.04305$. Gear selectivity $S(x)$ was a logistic function of length, with asymptote equal to 1 (full selectivity), length at the inflection point (where $S(x) = 0.5$) equal to 85.22 cm, and slope (with respect to length) at the inflection point $r = 0.05515$. These values are maximum likelihood estimates obtained using Pacific halibut catch data from years 1974 to 1986 for IPHC regulatory area 2AB. When these parameters were estimated, initial abundances and fishing mortalities were fixed at values corresponding to estimates from catch-age analysis. Catch data were generated for the same number of years used in the estimation (years = 13) and thus the initial abundances and fishing mortalities estimated for Pacific halibut were used in the simulations. Figure 3 shows the corresponding sequences of parameter values. The number of length observations (first sample) and age-length observations (second sample) simulated for each of the 13 years were respectively 10 000 and 3400, which is close to the average sizes of samples available for Pacific halibut (area 2AB) for those years. The range of ages went from age 6 (coded age $a = 0$) to age 20. Observations for coded ages above $a = 12$ were pooled into a single age category during the estimation trials. The parameter F_{IC} was set equal to 0.2104, the average of the F_t values, and the instantaneous coefficient of natural mortality M was set to 0.2. The procedure used to approximate the selectivity function corresponds to that which minimizes the cross-entropy between the normal, approximated posterior distribution of x, $\varphi_x(a+\tau, t+\tau)$, and the "true" posterior resulting from using the selectivity function $S(x)$. As explained in Deriso and Parma (1988), this implies choosing the polynomial coefficients b_1 and b_2 so that the mean and variance of x for the approximated and "true" posterior distributions match. Coefficient b_0 is then selected to assure also a perfect match of the survival parameter $p(a,t)$. The polynomial coefficients are thus age- and year-specific, because they are a function of F_t, and the parameters of $S(x)$ and $\varphi(x|a,t)$. The same procedure was used both when generating artificial catch data and in the estimation.

The program employed to maximize the likelihood function uses a modified version of the Marquardt algorithm. Convergence problems were encountered because effects of parameter changes are confounded. Thus, we used an alternative parameterization of the model which is more stable: β, the parameters of the initial size distributions ($E_x(0)$,$V_x(0)$, and F_{IC}), and three more parameters that correspond to moments of the hypothetical growth trajectory in the absence of size-selective harvest. These are the hypothetical mean, $E_x^o(6)$, and variance, $V_x^o(6)$, of x for coded age $a = 6$ (approximately the mean age in the catch), given respectively by equations (4.1) and (6), and the variance of the asymptotic log-length $V_x(\infty)$, given by equation (5).

A number of estimation trials were conducted and the following growth parameters were estimated in each trial: $E_x(0)$,$V_x(0)$,$E_x^o(6)$,$V_x^o(6)$,β and F_{IC}. The parameter $V_x(\infty)$ was given a different fixed value in each trial, so that the coefficient of variation of asymptotic length (equation (10)) would take values of 0, 5, 10,$\cdots$, 40%. The value of $CV(L_\infty)$ used in the simulation was 25%. The remaining model parameters were held fixed at their true values. The maximum log-likelihood was computed in each trial.

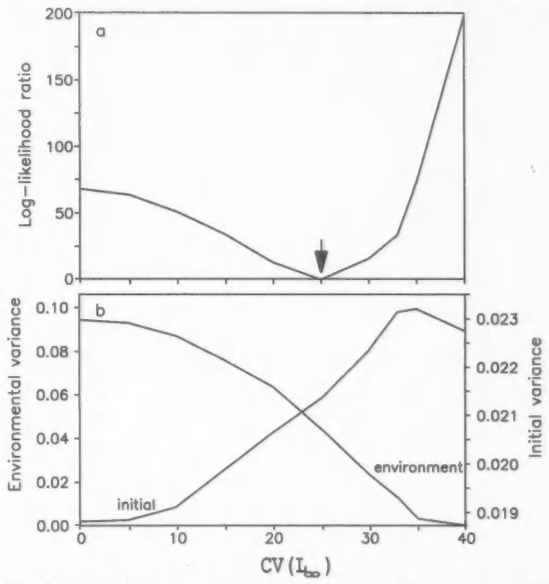

FIG. 4. Estimation of growth parameters from artificial catch data. (a) Log-likelihood ratio as a function of the value given to $CV(L_\infty)$, the coefficient of variation of asymptotic length, when the remaining growth parameters were estimated conditional on $CV(L_\infty)$. The arrow marks the value of $CV(L_\infty)$ used to simulate the data. (b) Effect of changing the value of $CV(L_\infty)$ on the estimates of V_U, the factor scaling the environmentally induced variability of growth increments, and of $V_x(0)$, the initial variance of log-length.

Results and Conclusions of Data Simulations

Results from the estimation trials allow us to explore the shape of the maximum likelihood surface across the $CV(L_\infty)$ dimension. Since simulated data correspond exactly to model predictions, their information content is exaggerated with respect to that of data generated by random sampling. While total sample sizes were very large (10 000 for the samples of length composition and 3400 for the samples of age-length), old age categories were poorly represented in the age-length samples (e.g. 30–50 individuals of age 18). As illustrated by the growth trajectories in Fig. 1, length distributions for old age categories contain most of the information for estimating the phenotypic contribution to growth variability. Assuming that observed distributions of size-at-age for old age categories are not affected by sampling errors is overly optimistic. Based on these considerations, we will only analyze the shape of the maximum likelihood surface, while dismissing the actual values of the log-likelihood ratio (i.e. the difference between the maximum log-likelihood functions computed at the true and fixed values of $CV(L_\infty)$).

The log-likelihood ratio increased steeply when $CV(L_\infty)$ was fixed at values larger than its true value, but the likelihood surface was flatter when $CV(L_\infty)$ was underestimated (Fig. 4a). The same was observed when estimation was carried out with real halibut data. Figure 4b shows how the remaining variance components adjust to compensate for the departure of $CV(L_\infty)$ from its true value. The two curves in the figure correspond to V_U, the coefficient scaling the environmental variance, and to $V_x(0)$, the initial variance of log-length. As expected, V_U absorbed most of the change in $CV(L_\infty)$: it decreased monotonically to almost 0 when $CV(L_\infty)$ increased up to 40%. The initial variance increased slightly when phenotypic variability was raised. This increase compensates for the effect that decreasing V_U has on the variance of x over young ages.

It is tempting to simply look at the basic growth model (1), that is $x_{a+1} = \alpha + \beta x_a + \epsilon_a$, and conclude that of course the random variables α and ϵ have a confounded effect on growth. This gives certainly an insight into the identifiability problem. Yet, as demonstrated throughout this paper, changes in phenotypic variation have some effect on modelled growth different from that due to environmental variation. Apparently, these differences are not large enough in our simulated data. Following individual growth trajectories, such as from individual otoliths, surely will help to identify the sources of variability more clearly.

4. Yield per Recruit and Reproductive Potential: Effects of Phenotypic Variability in Growth

The estimation trials conducted using Pacific halibut data indicate that the parameters representing the environmental and intrinsic components of growth variability cannot be identified with much certainty from standard catch data. The question that we address here is whether this uncertainty has any practical consequences in the determination of optimal levels of fishing on the basis of a yield per recruit analysis. We will consider the optimization problem consisting of maximizing the expected value of yield per recruit when size-selectivity of the fishing gear is held fixed. We focus on expected value of yield per recruit because this will be close to true mean yield per recruit when recruitment is large.

Following Deriso and Parma (1988), we assume that weight of an individual fish is related to its log-length by

$$W = me^{rx+\nu},$$

where $\nu \sim N(0,V_\nu)$, so that mean weight of fish of log-length x is given by $E_W(x) = m \exp\{rx + V_\nu/2\}$. Mean total yield harvested from a cohort over its entire life-span is given by

$$E[Y] = R \sum_{a=0}^{A} \int_{-\infty}^{\infty} E_W(x)(1-e^{-FS(x)})\varphi(x|a)l(a)dx,$$

where $l(a)$ is survival from age 0 to age a, given in Table 1, and R is the number of individuals of age $a = 0$. The optimal level of full-recruitment fishing mortality F_{max}, conditional on the selectivity function $S(x)$, can be found by maximizing $E[Y]/R$. The maximization is carried over a single control variable F. Instead of F_{max}, we can numerically approximate the more conservative level $F_{0.1}$, which is defined to be the level of F for which the marginal increase in $E[Y]/R$ due to a small increase in F is 10% of that at the origin (see Deriso 1987). The expression above for expected total yield can be rewritten as

$$(12) \quad E[Y] = R \sum_{a=0}^{A} (1-p(a))E_W^c(a)l(a),$$

where $(1-p(a))$ is the probability that a fish is caught at age a, given that it was alive before the harvest, and $E_W^c(a)$ is the mean weight of individuals caught at age a. At first sight this expression appears equivalent to a standard yield per recruit formulation, for the case where fishing takes place in a short period of time at the beginning of the year. In a standard deterministic analysis, the fraction of animals surviving the catch $p^d(a)$ would be given by

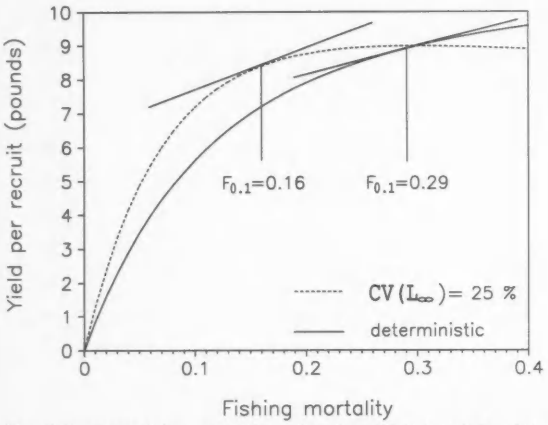

FIG. 5. Expected yield per recruit as a function of full-recruitment fishing mortality predicted by the stochastic model, and by a deterministic model in which age-specific selectivities and mean weights-at-age were fixed at the values predicted by the stochastic model for $F = 0.3$. Parameter values are equal to those used in Fig. 1.

$$p^d(a) = e^{-FS(a)},$$

where $S(a)$ is an age-dependent selectivity. In the stochastic model, instead,

$$p(a) = \int_{-\infty}^{\infty} e^{-FS(x)}\varphi(x|a)dx,$$

so it depends on F explicitly, as shown above, and implicitly, through the effects of size-selective harvest on the parameters of $\varphi(x|a)$. In addition, the values of $E_W^c(a)$ are also a function of F, whereas in the standard analysis mean weights-at-age are assumed fixed, and they are typically estimated from the catch means. When phenotypic variability in growth is high, an increase in F results in a progressive decrease in mean weight-at-age. This, in turn, affects total yield. Also, if egg production is proportional to individual weight, the effect of F on the reproductive potential of a cohort will also depend on the level of individual variability in growth.

The potential magnitude of these effects can be illustrated by contrasting the results obtained from the stochastic and deterministic yield per recruit analyses, conducted using parameter values for Pacific halibut. In both cases we used equation (12) to compute how expected yield varied as a function of F. For the deterministic analysis, we supposed that the stock had been subject to a sustained exploitation of $F = 0.3$, and that estimated age-specific selectivities ($S(a)$'s) and mean weights in the catch ($E_W^c(a)$'s) were equal to their expected values under that "historical" level of fishing mortality. Figure 5 shows the change in expected yield per recruit as a function of F predicted by the stochastic (dashed line) and deterministic (solid line) analyses. Computations are exactly the same when $F = 0.3$, the historical fishing level. For $F<0.3$, the deterministic treatment underestimates yield per recruit, and the opposite is true for $F>0.3$. This is a direct result of fishery-induced changes in growth pattern: weights-at-age for $F = 0.3$, used in the deterministic analysis, are smaller than those predicted for $F<0.3$, and they are larger than those for $F>0.3$. The indirect effect of the change in growth pattern due to size-selection on the vector of age-specific mortalities was negligible. The standard assumption that age-specific selectivities and mean weights-at-age in the catch are constant, independent of the level of F (i.e. the deterministic analysis) would, in this case, result in a gross overestimation of the level F_{max}. The levels $F_{0.1}$ computed in the two cases are also substantially different: $F_{0.1} = 0.16$ for the stochastic model and $F_{0.1} = 0.29$ for the deterministic model. If the stochastic model realistically represented the processes involved, fishing levels prescribed on the basis of the deterministic yield per recruit analysis could result in growth overfishing.

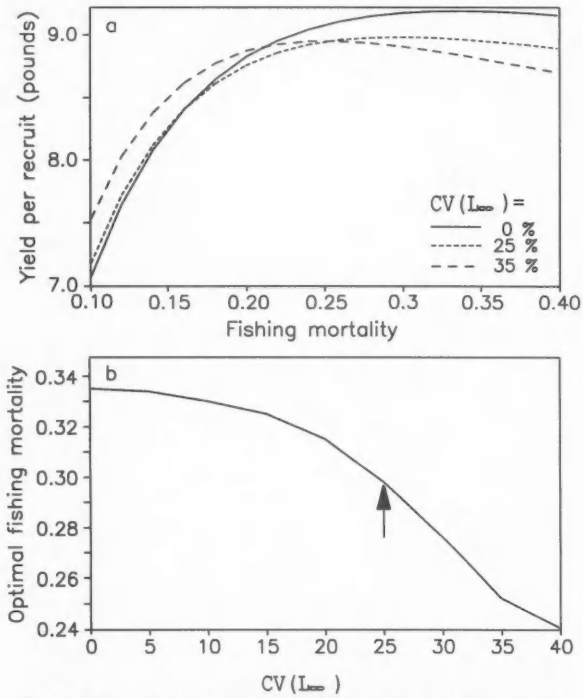

FIG. 6. Effects of phenotypic variability in growth on yield per recruit. (a) Expected yield per recruit as a function of full-recruitment fishing mortality for three levels of coefficient of variation of asymptotic length, $CV(L_\infty)$. (b) Fishing mortality for maximum yield per recruit as a function of $CV(L_\infty)$. Parameter values are maximum likelihood estimates conditional on $CV(L_\infty)$ obtained from artificial catch data. The arrow marks the value of $CV(L_\infty)$ used to generate the data; other parameter values were equal to those used in Fig. 1

Within the framework of the stochastic model, results are more encouraging. We used the parameter values obtained from the estimation trials explained earlier to explore the effects of changes in the relative contribution of extrinsic versus intrinsic sources of growth variability. In those trials, different sets of growth parameters were estimated by the maximum likelihood method for fixed $CV(L_\infty)$ values of 0, 0.05, ···, 0.40. A yield per recruit analysis was conducted for each set of conditional (on a given $CV(L_\infty)$) growth parameter estimates. Figure 6a shows the expected yield per recruit as a function of full-recruitment fishing mortality F for various levels of phenotypic variability. At low fishing rates, yield is an increasing function of $CV(L_\infty)$, and the trend reverses at higher levels of F. The value of F_{max} decreases monotonically when $CV(L_\infty)$ increases (Fig. 6b). The effect is minor when phenotypic variability is lowered below the actual value used to generate catch data (the value signalled by the arrow). When, on the other hand, values

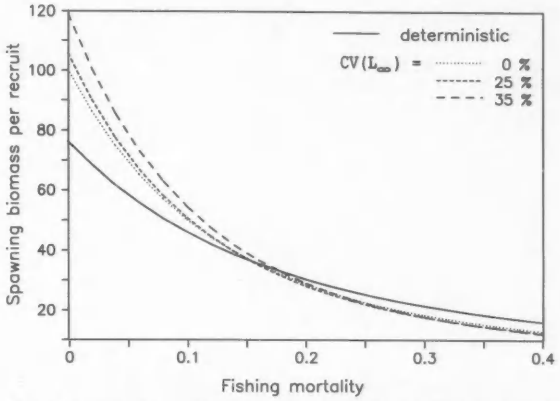

FIG. 7. Expected spawning biomass per recruit as a function of full-recruitment fishing mortality for three levels of $CV(L_\infty)$, the coefficient of variation of asymptotic length. Parameter values are maximum likelihood estimates conditional on $CV(L_\infty)$ obtained from artificial catch data.

of $CV(L_\infty)$ larger than the true one are forced, F_{max} decreases rather abruptly. Therefore, even if $CV(L_\infty)$ is set to zero, the stochastic model is closer to the model used in the simulations than the deterministic model.

In order to evaluate the effects of phenotypic growth variability and harvesting on mean reproductive potential of the individuals, we computed the value of spawning biomass per recruit as a function F for each set of growth parameters used earlier. Mean spawning biomass per recruit, $E[S]$, results from summing the products of expected biomass per recruit for each age a times the fraction of mature females $m(a)$ across all ages in the population; thus,

$$E[S] = \sum_{a=0}^{A} m(a)E_W(a)l(a),$$

where $E_W(a)$ is expected individual weight of animals of age a. The value of $E[S]$ would be proportional to expected egg production if fecundity were proportional to individual weight, and growth and survival parameters used were those for females. Values of $m(a)$ for Pacific halibut (IPHC regulatory area 2) were obtained from St-Pierre (1984); yet, this is a simplification since $m(a)$ likely depends on size.

In the absence of fishing, expected spawning biomass increased with the level of $CV(L_\infty)$ (Fig. 7, dotted lines). A maximum increase of 20% was computed when $CV(L_\infty)$ was raised from 0.0 to 0.35. Size-selective fishing counteracts this effect by depressing growth rate more strongly the higher the phenotypic component of growth variability. Spawning biomass was insensitive to changes in $CV(L_\infty)$ when F approached the F_{max} levels. As a consequence, the fishing rate that yields a constant value of spawning biomass per recruit, based on the stochastic model, is nearly independent of $CV(L_\infty)$, provided the values of $E[S]$ chosen are on the order of those expected in the population subject to exploitation. A larger bias was observed however when calculations were based on a deterministic model analogous to that used to compute yield per recruit (Fig. 7, solid line). As before, age-specific mean weights and selectivities were assumed constant, independent of F, and they were fixed at the levels predicted for $F = 0.3$, using mean weights-at-age in the catch as estimates of mean weights-at-age in the spawning population. For low levels of fishing mortality, mean spawning biomass computed in this way was lower than that based on the stochastic model (for any level of $CV(L_\infty)$); the trend again reversed at intermediate fishing levels.

The results indicate that neglecting the effect of size-selectivity on growth (i.e. the deterministic approach) may cause important biases in the estimates of spawning biomass and optimal fishing levels. On the other hand, when computations are based on the stochastic model, the effects of changing the relative contribution of extrinsic and intrinsic sources of growth variability is comparatively smaller, given that growth parameters are estimated conditional on the level chosen for $CV(L_\infty)$. It is worth emphasizing that the analyses above based on the stochastic model show how F_{max} and $E[S]$ vary across a range of values of $CV(L_\infty)$ that are relatively consistent with a specfic set of catch observations. The remaining parameter values and, in turn, the F_{max}'s in the graph are maximum likelihood estimates conditional on $CV(L_\infty)$. The effects are much stronger when $CV(L_\infty)$ is changed freely holding the other parameters fixed.

5. Discussion

The stochastic model analyzed is a generalization of the model developed by Deriso and Parma (1988). As such, it utilizes the results of the earlier model but further enhances its flexibility.

The growth treatment is innovative in the sense that growth variability results from both environmental and intrinsic sources. Previous stochastic growth models have attributed all growth variability to either one of the two sources. Individual growth increments as a function of size and age, and the resulting growth patterns for the cohort as a whole, are probabilistically described. Thus, the model is suitable for the analysis of data on length-at-age, as well as on growth increments from mark–recapture experiments. Standard growth models commonly used to estimate growth parameters from these two types of observations are not equivalent (Francis 1988b). Even though the models may be based on the same deterministic growth function, assumptions about growth variability made when fitting the models to data differ. Parameters estimated by the two approaches are therefore not comparable. The stochastic model proposed here, instead, can be applied to both types of data without modification of the underlying assumptions. Likelihood equations were developed to fit the model to length-at-age observations, and they could be similarly constructed to analyze data on length increments.

The incorporation of phenotypic variability allows for a more refined treatment of the effects of size-selective mortality on the dynamics of size and abundance. Consider the most common situation where selectivity is an increasing function of size. When variability of growth increments experienced by an individual are independent of its previous growth history, size-selective harvesting removes the largest individuals, but not those that grow intrinsically fastest. In contrast, when individuals have different growth potentials, the larger fish for a given age are expected to grow faster than average in the future, which amplifies the effects of size-selective mortality. Changes in mean growth, in turn, influence the amount of yield that can be obtained from the cohort. A standard assumption commonly made in yield per recruit analysis, namely, that mean weights-at-age are constant, independent of the fishing mortality rate can result in gross overestimation of optimal fishing levels.

Fishing rates for maximum average yield per recruit, estimated using the stochastic model, can heavily depend on how variability in growth is partitioned between extrinsic and intrinsic components. The sensitivity analysis, conducted using parameter estimates of Pacific halibut, showed that optimal fishing levels decreased with the level of phenotypic variability used in the computations. It is important to emphasize that the optimal fishing rate for each chosen level of phenotypic variability was computed using parameter estimates conditional on that level of phenotypic variability. Yield sensitivity would be larger if the level of variability due to intrinsic factors were varied while holding the remaining parameters constant.

The importance of the effects of size-selective mortality on mean growth rates depends on the extent to which individuals differ in their growth potential. Our experience with Pacific halibut data indicates that standard catch observations on age/length frequency distributions may contain little information about the relative contribution of environmental versus intrinsic sources of growth variability, at least as represented in the model. The growth pattern exhibited by Pacific halibut is almost linear, which contributes to confound the two variance components, $V_\epsilon(0)$ and $V_\alpha(0)$. This is best seen in the expression for the trajectory of $V_x(a)$ for the case of $\beta = 1$. Asymptotic growth patterns should be more informative than nonasymptotic ones, since variance of observed log-length for old fish would be closer to the variance of asymptotic log-length, which is assumed to represent intrinsic differences in growth rates. In general, however, sources of growth variability will be difficult to estimate from catch data, for catch data only provide information of size/age of individuals at time of capture. Data on individual growth trajectories, such as those obtained from back-calculated sizes from otoliths or scales, would be the most appropriate to explore this problem. Size-specific growth increments for animals that grew intrinsically fastest would be consistently above the expected increments for the population as a whole.

If variability in individual growth had a genetic basis, removing the larger fish would further imply selecting the slower-growing individuals as parents for the next generation. Aside from the relatively common cases where males and females have different growth patterns, information about the relative importance of extrinsic versus intrinsic sources of growth variability is scarce. The artificial selection of faster-growing phenotypes in aquaculture indicates that intraspecific differences in growth rate do have some genetic basis. Yet, estimates of heritability available for some fish species are moderate to low (Pitcher and Hart 1982; Kinghorn 1983; Weatherley and Gill 1987). Results of some breeding experiments are inconclusive due to the confounding of genetic effects with the effects of improved husbandry conditions or those of social interactions (Purdom 1979; Kirpichnikov 1981; Kinghorn 1983). A reduction of growth rate following size-selective fishing has been documented for several fish stocks (Ricker 1981; Wohlfarth 1986; Nelson and Soule 1987), although in most cases patterns are also consistent with other alternative explanations not involving genetic effects. More convincing results have been produced under experimental conditions by Silliman (1975).

Other approaches for detecting genetic responses to fishing have been discussed by Nelson and Soule (1987), who suggested that "either method would be more powerful if a model complete with estimates of selection differential and of heritability...were to make a predictive confirmation possible." The model proposed in this study could be easily modified to explore genetic selection effects. A discrete number of growth genotypes could be assumed (as was done by Favro et al. 1979), or the α parameter itself could be used to represent the genetic basis of growth variability.

As in the earlier version in Deriso and Parma (1988), the generalized model developed here can be used to estimate year-class strength and fishing mortalities from data on catch in biomass, and length/age distributions in the catch. Gain in flexibility, however, is achieved through the incorporation of additional parameters, with a consequent increase in the dimensions of the estimation problem. Although few parameters are involved in the dynamic equations, many parameters are needed to specify the initial size distributions (i.e. initial mean and variance of size for each of the year-classes present over the period considered). Certainly, the parameter space can be reduced by making more restrictive assumptions, such as those made in section 3. The fact that size distributions in the catch are shifted with respect to the distributions in the catch are shifted with respect to the distributions in the population (see Deriso and Parma 1988) prevents obtaining parameter values for the initial conditions directly from the catch moments. The large number of parameters involved is a major drawback of the alternative, discrete approach to incorporate growth variability. When males and females exhibit different growth patterns, such as is the case in Pacific halibut (Deriso and Quinn 1983), an option that is equivalent, in terms of number of parameters, to that used in section 3 is to place all the between-sexes variability in the asymptotic length. This may be preferable over the continuous approach when differences between sexes lead to bimodal distributions and, especially, if the sex of the fish sampled for age and size composition is known.

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Appendix A: Derivations for Growth Model with Individual Variability

Assume that the joint pdf of (x_a, α) is bi-variate normal with parameters $E_x(a)$, $V_x(a)$, $E_\alpha(a)$, $V_\alpha(a)$, and $\mathrm{Cov}_{x,\alpha}(a)$. In the absence of size-selective mortality, $E_\alpha(a) = E_\alpha(0)$, and $V_\alpha(a) = V_\alpha(0)$. The variable ϵ_a in the growth equation is normally distributed and independent of x and α; hence the joint pdf of $(x_a, \alpha, \epsilon_a)$ is three-variate normal. The vector (x_{a+1}, α) results from applying a linear transformation to the vector $(\alpha_a, \alpha, \epsilon_a)$ namely,

$$\text{(A.1)}\quad \begin{bmatrix} x_{\alpha+1} \\ \alpha \end{bmatrix} = \begin{bmatrix} \beta & 1 & 1 \\ 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} x_a \\ \alpha \\ \epsilon_a \end{bmatrix},$$

and, therefore, it also has a bi-variate normal distribution (Bickel and Doksum 1977). The recursive equations for updating the mean and variance of x follow directly from (A.1). The equation for updating the covariance parameter results from applying the properties of the covariance operator. Thus, if $\mathrm{Cov}[\cdot, \cdot\cdot]$ denotes the covariance between $(\cdot)$ and $(\cdot\cdot)$, the parameter $\mathrm{Cov}_{x,\alpha}(a+1)$ is equivalent to

$$\text{(A.2)}\quad \begin{aligned} \mathrm{Cov}[x_{a+1}, \alpha] &= \mathrm{Cov}[\alpha + \beta x_a + \epsilon_a, \alpha] \\ &= V_\alpha(0) + \beta \mathrm{Cov}_{x,\alpha}(a). \end{aligned}$$

Let $a = 0$ be the initial coded age. If the variance of ϵ_a is assumed constant, that is $V_\epsilon(a) = V_\epsilon$, then equations (2) in the text correspond to the mean and variance of x_a conditional on a given value of α. Notation can be changed to reflect that parameters are conditional on α as

$$E_{x|\alpha}(a) = \frac{\alpha}{1-\beta} + \left[E_{x|\alpha}(0) - \frac{\alpha}{1-\beta}\right]\beta^a \text{ and}$$

$$V_{x|\alpha}(a) = V_{x|\alpha}(0)\beta^{2a} + V_\epsilon\left[\frac{1-\beta^{2a}}{1-\beta^2}\right].$$

The unconditional parameters can be obtained from the conditional ones by applying the theorem that states that, for any two random variables u and v,

$$\text{(A.3)}\quad \begin{aligned} \mathrm{E}[\mu] &= \mathrm{E}_v[\mathrm{E}[\mu|v]], \text{ and} \\ V[u] &= E_v[V[u|v]] + V_v[E[u|v]], \end{aligned}$$

where $E_v[\cdot]$ and $V_v[\cdot]$ denote respectively the expected value and variance of $(\cdot)$ taken with respect to the distribution of v (Bickel and Doksum 1977). In our case, x takes the role of u and α takes the role of v. The unconditional mean of x_a results simply from replacing α and $E_{x|\alpha}(0)$ in the expression for $E_{x|\alpha}(a)$ by their expected values. The unconditional variance of x_a is

$$\text{(A.4)}\quad V_x(a) = V_\alpha[E_{x|\alpha}(a)] + E_\alpha[V_{x|\alpha}(a)].$$

The first term on the right-hand side of the equation above is given by

$$\left[\frac{1-\beta^a}{1-\beta}\right]^2 V_\alpha(0) + \beta^{2a} V_\alpha[E_{x|\alpha}(0)] + 2\mathrm{Cov}[E_{x|\alpha}(0), \alpha]\beta^a \times \left[\frac{1-\beta^a}{1-\beta}\right],$$

and the second term by

$$V_\epsilon\left[\frac{1-\beta^{2a}}{1-\beta^2}\right] + \beta^{2a}(V_x(0) - V_\alpha[E_{x|\alpha}(0)]).$$

Notice that

$$\begin{aligned} \mathrm{Cov}[E_{x|\alpha}(0), \alpha] &= \mathrm{Cov}\left[E_x(0) + \frac{\mathrm{Cov}_{x,\alpha}(0)}{V_\alpha(0)}(\alpha - E_\alpha(0)), \alpha\right] \\ &= \mathrm{Cov}_{x,\alpha}(0). \end{aligned}$$

Substitute the above expressions into (A.4) to obtain equation (4.2) after cancellations.

The age-dependent trajectory of the covariance parameter (equation (4) in the text) follows after applying a times the recursive equation (A.2) with initial conditions $\mathrm{Cov}_{x,\alpha}(0)$ and $V_\alpha(0)$.

Appendix B: Derivations for Growth and Abundance under Size-Selective Mortality

Here we derive recursive equations for the parameters of the bi-variate normal pdf of (x, α) as modified by size-selective harvest over a single fishing season. Shifts in the mean and variance of x are given by equations (a) and (b) in Table 1. Thus, we shall just focus on the effect of fishing on the marginal distribution of α and covariance between α and x.

If the joint pdf of (x, α) is bi-variate normal with parameters $E_x(a,t)$, $V_x(a,t)$, $E_\alpha(a,t)$, $V_\alpha(a,t)$, and $\mathrm{Cov}_{x,\alpha}(a,t)$, and the covariance matrix is nonsingular, the conditional pdf of α given x is normal with mean and variance, respectively,

$$E_{\alpha|x}(a,t) = E_\alpha(a,t) + \frac{\mathrm{Cov}_{x,\alpha}(a,t)}{V_x(a,t)}\,(x - E_x(a,t)), \text{ and}$$

(B.1)

$$V_{\alpha|x}(a,t) = V_\alpha(a,t) - \frac{\mathrm{Cov}_{x,\alpha}(a,t)^2}{V_x(a,t)}$$

(Bickel and Doksum 1977). Notice that the conditional mean of α is linear on x, and the conditional variance of α does not depend on x; recall that the symbols V_x and $\mathrm{Cov}_{x,\alpha}$ have x as notation and not to indicate functional dependence on x. This will later facilitate the application of (A.3) to obtain the unconditional mean and variance of α from the conditional parameters (α plays the role of u and x plays the role of v). As shown earlier, the pdf of α conditional on x is not affected by size-selective harvest over a single fishing season (equation (8) in the text). The conditional parameters prior to the harvest (those given by (B.1)) can therefore be used when applying (A.3) to obtain the unconditional parameters of the posterior distribution of α. Thus, equation (9.1) for the unconditional mean of α after the harvest, $E_\alpha(a+\tau, t+\tau)$, results from taking the expectation of $E_{\alpha|x}(a,t)$ with respect to x at time $t+\tau$; that is

$$E_\alpha(a+\tau, t+\tau) = E_x[E_{\alpha|x}(a,t)],$$

where $x \sim \varphi(x|a+\tau, t+\tau)$. Likewise, the unconditional variance of α at time $t+\tau$ is

$$V_\alpha(a+\tau, t+\tau) = E_x[V_{\alpha|x}(a,t)] + V_x[E_{\alpha|x}(a,t)],$$

where $E_x[\cdot]$ and $V_x[\cdot]$ correspond, respectively, to expected value and variance of $(\cdot)$ computed with respect to x at time $t+\tau$. As the conditional variance of α is independent of x, the argument of the expectation in the first term is constant. After substituting (B.1) into the equation above we obtain

$$V_\alpha(a+\tau, t+\tau) = V_\alpha(a,t) - \frac{\mathrm{Cov}_{x,\alpha}(a,t)^2}{V_x(a,t)} + \left[\frac{\mathrm{Cov}_{x,\alpha}(a,t)}{V_x(a,t)}\right]^2 \times V_x(a+\tau,t+\tau).$$

Equation (9.2) in the text follows after rearrangement.

In order to update the covariance parameter, we use again the fact that, for any given x,

$$E_{\alpha|x}(a+\tau, t+\tau) = E_{\alpha|x}(a,t).$$

These conditional means are linear functions of x; hence, for the equality to hold, the slopes of the respective functions have to coincide. Then,

$$\frac{\mathrm{Cov}_{x,\alpha}(a+\tau, t+\tau)}{V_x(a+\tau, t+\tau)} = \frac{\mathrm{Cov}_{x,\alpha}(a,t)}{V_x(a,t)},$$

where $V_x(a+\tau, t+\tau)$ is as given in Table 1. Solving for the updated covariance gives equation (9.3) in the text.

Appendix C: Likelihood Equations when a Discrete Number of Growth Morphs is Separately Modelled

Here we generalize the estimation theory in Deriso and Parma (1988) to incorporate the existence of a discrete number of growth morphs in the population. For simplicity we present the equations for the case where the growth morphs correspond to the two sexes. The dynamics of growth and abundance can be modelled independently for each sex, and sex-specific components can be combined in order to obtain the likelihood of the observations made each year. These observations consist of: (1) length distribution of animals in a random sample of the catch, (2) length and age of fish in a subsample of the sample in (1), and (3) total catch in numbers or biomass. The likelihood has then three components, one for each set of observations. The equations are modified simply by summing components across growth morphs. Suppose f and m denote respectively females and males; then the expected abundance of fish of age a and sex s in year t is given by

$$E_N(a,t,s) = R_{t-a,s}\,l(a,t,s),$$

where $R_{t-a,s}$ is abundance of fish of reference age 0 and sex s in year $t-a$, and $l(a,t,s)$ is the proability of survival from age 0 to age a for fish of sex s. Also, the probability that a randomly selected animal in the catch in year t is of age a and sex s can be approximated as

$$P^c_{a,t,s} = \frac{E_N(a,t,s)(1-p(a,t,s))}{\sum_{i=0}^{A}[E_N(i,t,f)(1-p(i,t,f)) + E_N(i,t,m)(1-p(i,t,m))]},$$

where $p(a,t,s)$ is the probability that a fish of sex s and age a avoids capture in year t. The likelihood of the observations can be constructed as in Deriso and Parma (1988), just by making the substitutions that follow. In the first component, the pdf of x in the catch of year t, $f^c(x|t)$, needs to be replaced by

$$f^c(x|t) = \sum_{a=0}^{A}[P^c_{a,t,f} f^c(x|a,t,f) + P^c_{a,t,m} f^c(x|a,t,m)],$$

where $f^c(x|a,t,s)$ denotes the pdf of log-length of fish of age a and sex s in the catch of year t. In the second likelihood component, the joint probability that an animal in the subsample is of age a and log-length x is now given by

(C.1) $$f^c(x|a,t)P^c_{a,t} = P^c_{a,t,f} f^c(x|a,t,f) + P^c_{a,t,m} f^c(x|\mathrm{a,t,m}).$$

If total catch is given in numbers, its distribution can be approximated by a normal with parameters

$$E_C(t) = E_C(t,f) + E_C(t,m) \quad \text{and}$$
$$V_C(t) = V_C(t,f) + V_C(t,m),$$

where $E_C(t,s)$ and $V_C(t,s)$ are the sex-specific mean and variance of catch in numbers, computed separately with equations (11). When, instead, the biomass of the catch is known, equation (C.1) can be substituted into the equations for the mean

and variance of individual weight of the animals in the catch given in Deriso and Parma (1988). These are needed to compute the mean and variance of the catch in biomass. Again, a normal approximation for the distribution of total catch in biomass can be used to construct the third likelihood component.

Appendix D: Glossary of Functions and Parameters

a = coded age where $a = 0$ corresponds to youngest age of exploitation
α = parameter of the stochastic growth model
b_0, b_1, b_2 = coefficients of a polynomial approximation of $S(x)$
β = slope parameter of the stochastic growth model
C_t = random variable for total catch in numbers in year t
$\mathrm{Cov}_{x,\alpha}(a,t)$ = covariance of α and log-length x for a cohort of age a at the start of year t
$CV(L_\infty)$ = coefficient of variation of asymptotic length
$E_\alpha(a,t)$ = mean of α for a cohort of age a at the start of year t
$E_{\alpha|x}(a,t)$ = mean of α conditional on log-length x for a cohort of age a at the start of year t
$E_{x|\alpha}(a,t)$ = mean log-length conditional on the growth parameter α for a cohort of age a at the start of year t
$E_x(a,t)$ = mean log-length of a cohort of age a at the start of year t
$E_C(t)$ = expected number of individuals in the catch in year t
$E_C(t,s)$ = expected number of individuals of sex s in the catch in year t
$E_N(a,t)$ = expected number of individuals in the population of age a at the start of year t
$E_N(a,t,s)$ = expected number of individuals in the population of age a and sex s at the start of year t
$E[S]$ = expected spawning biomass per recruit
$E[Y]$ = mean yield per recruit
$E_W(x)$ = mean weight of individuals of log-length x
$E_W^c(a)$ = mean weight of individuals of age a in the catch
ϵ_a = normal random variable with 0 mean and variance $V_\epsilon(a)$ representing environmentally induced variability of growth increments in individuals of age a
$f(\cdot)$ = general notation for a pdf
$f^c(x|a,t)$ = pdf of log-length x for fish of age a in the catch in year t
$f^c(x|a,t,s)$ = pdf of log-length x for fish of age a and sex s in the catch in year t
$f^c(x|t)$ = pdf of log-length in the catch in year t
F_{IC} = fishing mortality used to generate initial parameters for size distributions of the cohorts in year $t = 1$
$F_{\max}$ = full-recruitment fishing mortality for maximum yield per recruit conditional on a given size-selectivity function
F_t = full-recruitment fishing mortality in year t
$l(a,t)$ = cumulative probability of survival from reference age 0 to age a
$l(a,t,s)$ = cumulative probability of survival from reference age 0 to age a for fish of sex s
Λ = joint log-likelihood of data collected for T years
m = parameter of the allometric weight-length function
$m(a)$ = fraction of mature females of age a
M = coefficient of natural mortality
NL = number of length categories in the samples of the catch.
ν = normal weight random variable with 0 mean and variance V_ν
$p(a,t)$ = probability a randomly selected individual of age a avoids capture in year t
$p(a,t,s)$ = probability a randomly selected individual of age a and sex s avoids capture in year t
$P_s(a,t)$ = probability a randomly selected fish in the population in year t is of age a and sex s
$P^c_{a,t}$ = probability that a randomly selected fish in the catch in year t is of age a
$P^c_{a,t,s}$ = probability that a randomly selected fish in the catch in year t is of age a and sex s
$pr(\cdot)$ = probability that event $(\cdot)$ occurs
$\varphi(x|a,t)$ = normal pdf with mean $E_x(a,t)$ and variance $V_x(a,t)$, evaluated at x
$\varphi(x|a,t,s)$ = normal pdf of x for fish of age a and sex s at the beginning of year t
r = power coefficient of the allometric weight-length function
R_{t-a} = abundance of reference age 0 fish in year $t - a$
$R_{t-a,s}$ = abundance of fish reference age 0 and sex s in year $t - a$
$S(x)$ = selectivity of fishing mortality for fish of log-length x
t = beginning of year t
$t + \tau$ = beginning of the second part of year t, after fishing
$V_\alpha(a,t)$ = variance of α for a cohort of age a at the start of year t
$V_{\alpha|x}(a,t)$ = variance of α conditional on log-length x for a cohort of age a at the start of year t
$V_\epsilon(a)$ = variance of the normal growth random variable ϵ_a
$V_C(t)$ = variance of number of animals in the catch in year t
$V_C(t,s)$ = variance of number of animals of sex s in the catch in year t
$V_N(a,t)$ = variance of number of animals of age a in the population in year t
$V_{x|\alpha}(a,t)$ = variance log-length conditional on the growth parameter α for a cohort of age a at the start of year t
$V_x(a,t)$ = variance of log-length for fish of age a at the start of year t
V_U = parameter scaling $V_\epsilon(a)$
W = weight of an individual fish
x_a = natural logarithm of length of an individual of age a

Pattern of Solute Movement from Snow into an Upper Michigan Stream

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Precipitation, snowpack, snowmelt, and streamwater samples were collected in a small gauged watershed draining into Lake Superior during winter 1987–88 to assess the importance of snowmelt pattern and meltwater pathways in the occurrence of solute pulses in streamwater. The snowpack along the south shore of Lake Superior can contain 50% of annual precipitation inputs and 38% of annual ionic inputs including moderate levels of strong acids. Throughout winter, thawed surface soils and small but steady snowpack moisture release promoted movement of snowpack solutes to surface mineral soils. Preferential elution of K^+, NH_4^+, and H^+ from the snowpack occurred with the initial thaw. Most ions exhibited pulses in snowmelt. Transport of snowpack solutes to the stream during snowmelt was through near-surface soil macropores and overland flow. For those ions with concentrations higher in the snowpack than in the premelt streamwater, K^+, NH_4^+, and H^+, the earliest snowmelt pulses had the greatest influence on streamwater chemistry. Unlike other portions of the region with resistant bedrock, the widespread presence of alkaline glacial till provides excess stream acid neutralization capacity (ANC) to buffer acidic inputs. Peak winter streamwater ANC reduction was caused principally by spring melt dilution of base cations and associated alkalinity, constant high SO_4^{2-} levels, and an increase in NO_3^-. The maximum reduction in stream ANC was concurrent with overland flow. Relative to its snowmelt concentration, NO_3^- was highest in streamwater with some stream input likely the result of nitrification and N mineralization.

Des échantillons des précipitations, de la neige accumulée, de l'eau de fonte de neige et de l'eau du cours d'eau ont été prélevés dans un petit bassin versant équipé de jauges et se drainant dans le lac Supérieur au cours de l'hiver 1987–88, afin d'évaluer l'importance du mode de fonte de la neige et des trajectoires suivies par l'eau de fonte sur l'apparition ponctuelle de fortes concentrations de substances en solution dans l'eau courante. La neige accumulée le long de la rive sud du lac Supérieur peut contenir 50% des précipitations annuelles et 38% des ions annuels, y compris des niveaux moyens d'acides puissants. Tout au cours de l'hiver, les sols superficiels dégelés et l'échappement faible, mais continu, d'humidité de la neige accumulée ont encouragé le déplacement des substances en solution de la neige accumulée vers les sols minéraux superficiels. Une élution préférentielle du K^+, du NH_4^+ et du H^+ de la neige accumulée s'est produite au cours de la fonte initiale. La plupart des ions ont présenté des maximums dans l'eau de fonte de la neige. Le transport des substances en solution provenant de la neige accumulée vers le cours d'eau au cours de la fonte s'est produit dans les macropores du sol près de la surface et sous forme de ruissellement. Pour les ions dont les concentrations étaient plus élevées dans la neige accumulée que dans l'eau du cours d'eau, avant apport des eaux de fonte, K^+, NH_4^+ et H^+, les premières apparitions des fortes concentrations d'eau de fonte de la neige avaient la plus grande influence sur la chimie de l'eau des cours d'eau. Contrairement aux autres zones de la région, qui reposent sur le socle, la présence généralisée d'un till glaciaire alcalin fournit au cours d'eau un pouvoir neutralisant des acides (PNA) très important pour tamponner les apports acides. La plus importante diminution du PNA des eaux courantes, qui se produit en hiver a été principalement causée par la dilution printanière des cations basiques (baisse de l'alcalinité), des niveaux constamment élevés de SO_4^{2-} et une augmentation du NO_3^-. La réduction maximale du PNA du cours d'eau s'est produite de concert avec le ruissellement. Par rapport à sa concentration dans l'eau de fonte, le NO_3^- était plus abondant dans le cours d'eau, une partie de l'apport résultant probablement de la nitrification et de la minéralisation du N.

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Moderate to high inputs of acidic deposition have been documented throughout the Great Lakes basin (Glass and Loucks 1985). Superimposed on chronic acidification is episodic acidification after rain or snow. The seasonal strong acid inputs to streams and lakes resulting from snowmelt have been documented in the "acid sensitive" eastern portions of the region (Jeffries et al. 1979; Kelso et al. 1986).

Lake Superior rarely if ever freezes over. This results in large snow accumulations along the lake's south shore (Stottlemyer 1987). Because of the elevated acid neutralization capacity (ANC) in scattered alkaline glacial till, this area is considered less sensitive to direct acidic inputs than portions of the region dominated by precambrian granites and shallow nonalkaline soils (Norton 1982; Stottlemyer 1982). However, the Lake Superior basin is characterized by relatively small moderately sloped watersheds in which the runoff is rapid, increasing the potential for solute "pulses" to aquatic ecosystems. This potential is enhanced by the presence of larger snowpacks and

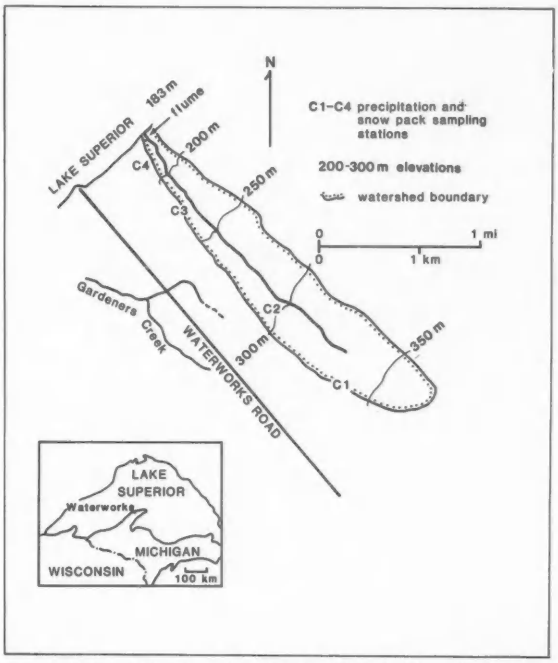

FIG. 1. Calumet Experimental Watershed (stippled boundary), Keweenaw Peninsula of Michigan, a 176-ha watershed draining into Lake Superior.

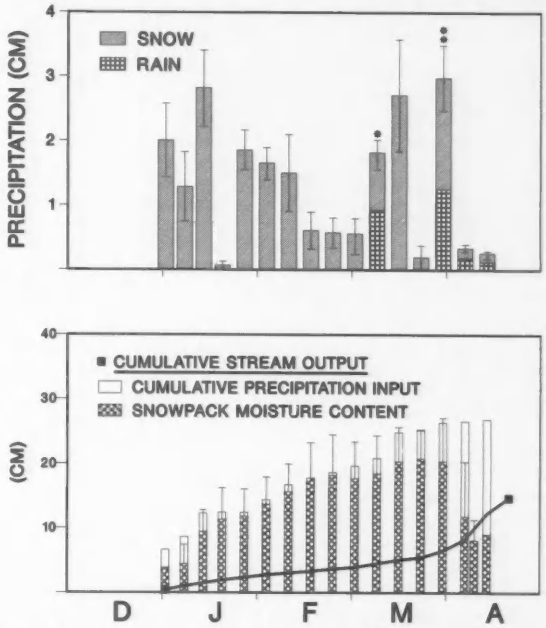

FIG. 2. Weekly average SWE, cumulative precipitation inputs, cumulative stream discharge,and weekly precipitation input as rain or snow for winter 1987–88. SWE brackets indicate one standard deviation. One asterisk, March 5 rain; two asterisks March 24 rain.

solute loads than occur in other sections of the region (Cadle et al. 1984; Semkin and Jeffries 1986; Stottlemyer 1987).

Peak snowpack water equivalent (SWE) often approaches 50% of annual precipitation inputs (Stottlemyer 1987). About 50% of annual runoff occurs during April and May (Miller et al. 1984)) which is comparable with values observed in the Adirondack Mountains (Troutman and Peters 1982) and Hubbard Brook in New Hampshire (Likens et al. 1977). Complicating the question of episodic acidification associated with snowmelt are preiodic thaws which can remove a large fraction of solutes prior to peak snowmelt, and natural variation which can increase inputs 2× from year to year (Stottlemyer 1987).

The concentration of SO_4^{2-} relative to NO_3^- in precipitation generally declines in winter (Johannes et al. 1985), and in portions of Lower Michigan the snow concentration of NO_3^- may equal that of SO_4^{2-} (Cadle et al. 1984). In northeastern United States studies, episodic aquatic acidification has generally been associated with NO_3^- (Rascher et al. 1987). However, in the Lake Superior Basin SO_4^{2-} concentration (equivalent basis) in precipitation is 2× that of NO_3^- (NADP 1987), and in the larger snowpacks along Lake Superior the SO_4^{2-} load in the snowpack can exceed NO_3^- by >2× (Stottlemyer 1987). Assimilation and soil adsorption are not significant in retaining SO_4^{2-} inputs (Stottlemyer and Hanson 1989), but biological assimilation of NO_3^- during late spring snowmelt may reduce its role in episodic acidification.

In view of the importance of NO_3^- and SO_4^{2-} input and loading in the snowpack, it appears that a better understanding of the processes involved in solute transport from the snowpack, forest floor, and soils to the stream or lake is necessary to assess the potential impacts of such anthropogenic inputs to aquatic ecosystems. The objectives of this study were to (1) relate seasonal change in precipitation chemistry and amount to snowpack solute concentration and load, (2) identify the chemical changes which occur as snowmelt passes through the forest litter layer and mineral soils to a stream in a representative small first-order watershed, and (3) assess possible differences in solute pathways during initial and later snowmelt releases.

Site Description and Methods

The study area is a small (176 ha) first-order watershed vegetated by 60-yr old sugar maple (*Acer saccharum*) and white birch (*Betula papyrifera*) near Calumet, Michigan, United States (Fig. 1). The watershed is adjacent to Lake Superior, has a northwest aspect and uniform slope varying in elevation from about 190 to 375 m above mean sea level. Its bedrock is Precambrian metamorphic Portage Lake Volcanics (andesite and basalt) overlain with alkaline glacial till and old beach deposits with a varying depth of 2–5 m. Soils are typic haplorthods, sandy, and mixed.

From 1980 to 1987 annual precipitation in the watershed averaged 95 ± 12 cm (range 78–113 cm). Winter precipitation, defined as that which occurred from December 1 to March 31, averaged 41% of annual precipitation. Annual precipitation was less and winter precipitation greater than that observed east of Lake Superior (Semkin and Jeffries 1986). On average, permanent snowcover began the first week in December and was gone by the third week in April.

Precipitation during winter 1987–88 was 32% of annual input (hydrologic year), and the peak mean SWE was 20.7 cm (Fig. 2). This was much below the 1980–87 average of 30.1 ± 8.5 cm (range 19–47 cm). The duration of the 1987–88 snowpack

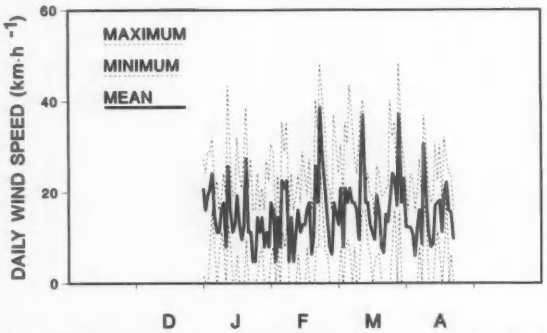

FIG. 3. Mean, minimum, and maximum daily wind speed ($km \cdot h^{-1}$), NOAA weather station, Houghton County Airport, MI.

was a month less than the 1980–87 average. Maximum mean SWE occurred the fourth week in March, about 1 wk later than average. The topographic relief of the watershed was associated with a significant ($P<0.001$, two-way ANOVA, Student-Newman-Keuls) increase in snowfall (station C1 = 27.2 cm, C4 = 19.9 cm) with elevation.

To aid in the interpretation of our results, we required information on wind. These data (Fig. 3) were obtained from the nearby (8 km) Houghton County NOAA weather station, which has an elevation similar to Station C1. The close proximity of this weather station to our watershed and the very uniform topography between the two locations increases the likelihood that there are similarities in surface winds. These data are used primarily to explain some of the discrepancies between cumulative precipitation inputs and SWE (Fig. 2).

Stream discharge has been gauged since fall 1979. Discharge has been measured using a 30-cm wide Parshall flume equipped with a Stevens F recorder. Use of Parshall flumes, which generate little head during most flow conditions, minimize possible change in local hydrologic pathways. Due to an almost impervious soil layer (ortstein) at 1.0–1.3 m depth, lateral soil water movement appears confined to near-surface layers.

Four monitoring stations were located at intervals of increasing elevation in the watershed (C4 (190 m) near the mean elevation of Lake Superior, C3 (240 m), C2 (295 m), and C1 (350 m), Fig. 1). From 1980 to 1985 each station was equipped with a bulk collector (36-cm diameter) to measure both precipitation quality and quantity. No significant difference in precipitation quality among stations was observed during that period, but precipitation amount did vary. Thus, in winter 1987–88 we used the same collector set-up but only determined precipitation quality at Station C1. The collectors were not shielded since the comparison collectors, National Atmospheric Deposition Program (NADP) station MI99, located 15 km from the watershed, were not shielded. Precipitation amount is recorded on site during summer.

A transect (five sampling points) was established at each station where SWE and depth were determined using a Mount Rose sampler. Samples for chemical analyses were collected in a 10-cm-diameter PVC tube. These snowpack sampling stations were deliberately located in openings to minimize canopy debris in the collectors which, upon melting the snow sample, could contribute to ion concentration. We have measured throughfall in the watershed for two winters and found no significant alteration of precipitation chemistry by the forest canopy (highest possible alteration was for NO_3^-, $0.05<P<0.65$) (Stottlemyer 1987). This would be expected in a watershed with few conifers and low estimated dry deposition (Glass and Loucks 1986).

In fall 1987, a fifth SWE transect and sampling station was established between stations C3 and C4 about 20 m from the stream. Triplicate snow and soil lysimeter plots were located here. Each snowpack lysimeter consisted of a 2×3 m external cedar frame 15 cm in height and 2 cm thick. A 0.15-mm polyethylene sheet was placed directly on the forest floor following leaf fall and attached to the frame. Melt waters were directed by PVC tubing to a central 1.5 m deep pit with insulated cover. Within the pit, tipping bucket raingages recorded snowmelt rates and volume from each snow lysimeter. Pit temperature and the rate and timing of snowmelt were recorded on a Licor 1000 datalogger. We elected not to disturb the forest floor to place any lysimeter immediately beneath the organic layer, or place any potential insulating material, as wood, beneath the snow lysimeters because of the likely change in heat transfer from the soil-forest litter layer to the snowpack. Experience in past winters has shown disturbance of the litter layer and/or placing plywood or thick plastic on the forest floor can significantly retard snowpack melt relative to that in the immediate area.

Triplicate soil tension lysimeter plots were located each in close proximity to one of the snow lysimeters. Each plot consisted of three lysimeters (ceramic cups, PVC tube, Soil Moisture Corp.) at both 15 (A and E) and 30 cm (Bhs) soil depths. Additional plot instrumentation included a datalogger to record mean daily snowpack temperature at 10 and 40 cm above the forest floor, soil temperature at 5 cm depth, daily mean and maximum/minimum air temperature; solar radiation; and a groundwater well equipped with a Stevens F float gauge for monitoring change in water table height.

During snowmelt, grab samples for chemical analyses were collected in linear polyethylene amber bottles from each snow lysimeter during the middle (16:00–17:00 h) of the daily melt period. When meltwater release rates became more variable sampling frequency was increased. Beginning in February, soil lysimeters were sampled weekly until peak snowmelt at which time they were sampled about every 3 d.

As a minimum, precipitation, snowpack, and stream samples were collected weekly on Tuesday afternoon. During snowmelt, stream samples were collected more frequently. In earlier years of study on this site, stream samples were collected at a 2- or 4-h interval during the snowmelt period with a Manning autosampler, and a continuously recording pH meter (Analytical Instruments Model 30WP) was in place. Based upon the results of this more intensive sampling and the consistent diurnal pattern of stream discharge during spring runoff, for the present study we sampled the stream daily at both the low and high discharge rates. We sampled more frequently when the stream discharge pattern became more variable.

Stream water samples were collected just above the flume using amber linear polyethylene 500-mL bottles, and stream temperature was recorded manually with a Fisher thermometer. Stream samples were not frozen prior to laboratory analyses.

Samples were immediately brought into the laboratory. Snow samples were melted at room temperature in carefully rinsed, covered polyethylene containers. PH, specific conductance, and alkalinity (titration with 0.02N H_2SO_4 to pH 4.5) were determined as soon as samples reached room temperature. Filtered (0.45-μm) subsamples were refrigerated (2°C) and chemical analyses for Ca^{2+}, Mg^{2+}, Na^+, K^+, NH_4^+, Cl^-, NO_3^-,

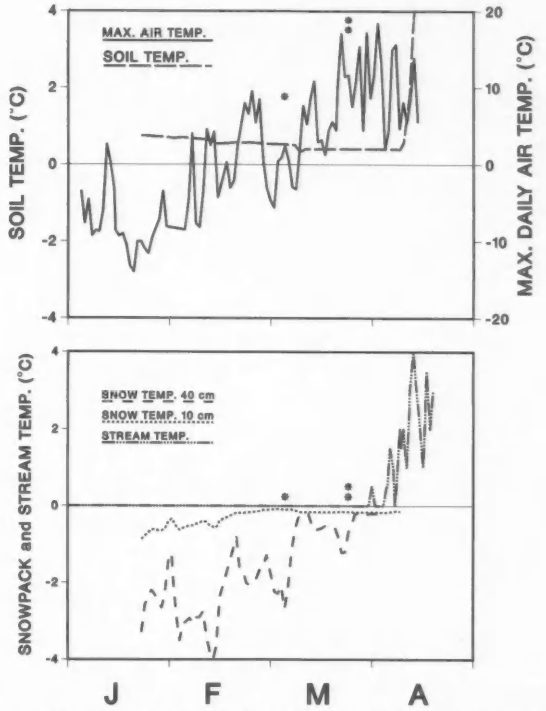

FIG. 4. Temperature of air (daily maximum), soil at 5-cm depth, snowpack at 10 and 40 cm above soil surface, and streamwater. One asterisk, March 5 rain; two asterisks, March 24 rain.

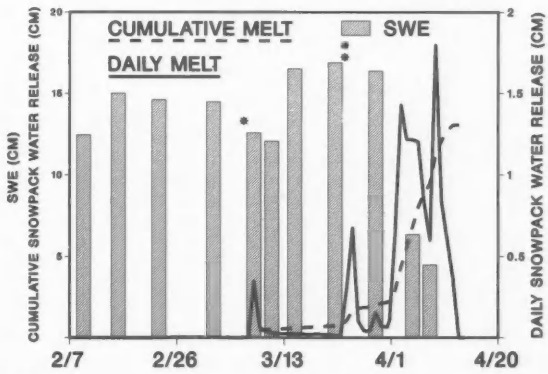

FIG. 5. Lysimeter plot SWE, and daily and cumulative snowmelt for the 55-d melt period. One asterisk, March 5 rain; two asterisks, March 24 rain.

PO_4^-, and SO_4^{2-} were conducted using ion chromatography (Dionex Model 2020).

Results

Precipitation and Hydrology

Most precipitation input remained in the snowpack for the first 9 wk (Fig. 2). There was little evidence that wind resulted in any consistent underestimation of winter precipitation input.

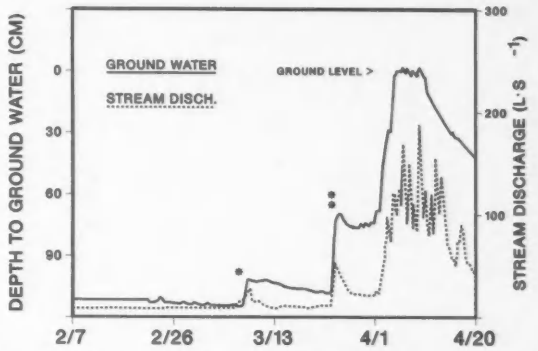

FIG. 6. Depth to groundwater and stream discharge during snowmelt period. One asterisk, March 5 rain; two asterisks, March 24 rain.

The NOAA data indicated that wind speeds <15 km·h^{-1} prevailed (Fig. 3). Snow drifts were seldom noted at most stations. The standard deviation of replicate snowcore SWE's, expressed as a percentage of the mean, was rarely >25% except during spring melt, and much of this variation was accounted for by input variation with elevation. However, on occasion, as during the middle of February, wind did appear to be a factor in underestimating precipitation input. In the second and third weeks of February the SWE increased without an equivalent increase in precipitation input (Fig. 2), and the standard deviation, expressed as a percentage of mean SWE, exceeded the previous weekly average by $>1.5\times$. During the third week daytime winds were often in excess of 30 km·h^{-1}. This along with the increased variation in precipitation amounts during this period suggests the likelihood of a varying loss in precipitation collector efficiency.

A midwinter thaw, beginning in late February (Figs. 4 and 5), accompanied by almost 1.0 cm of rain on March 5 (Fig. 2), resulted in an isothermal snowpack and net loss of 1.9 cm of SWE. The stream responded slightly to this initial thaw by increasing flow for about 1 wk during which an additional 0.04 cm above base flow was lost from the watershed (Fig. 6). Thus little of the moisture released in the initial thaw left the watershed as surface flow, and it likely served to recharge the groundwater table which increased 13 cm in height. Most of this recharge remained until the following thaw during the week of March 20.

Following the initial thaw, the maximum air temperature generally remained below freezing for the period March 1–11. The mean watershed precipitation input was 5.2 cm, and the mean SWE increased 3 cm (4 cm at the snow lysimeters). The difference between input and SWE during this period likely reflects continued steady snowpack losses due to thawed soils and to increased sublimation. With initiation of the second thaw, beginning on or about March 20, the snowpack rapidly became isothermal, and there was a sharp but isolated peak in snowmelt rate of 0.65 cm·d^{-1} (Figs. 4 and 5). The snowpack remained isothermal after March 26, although the temperature near its surface fell somewhat on cold nights. The subsequent freeze–thaw cycle, an isothermal snowpack, and rain input (Fig. 2) set the stage for the rapid snowmelt, snowpack ion loss, and runoff the following week.

During the last week of March mean precipitation input was 3 cm of which 1.3 cm was rain (Fig. 2). The highest sustained snowmelt period immediately followed this rain input, and

TABLE 1. Mean ion concentration ($\mu eq \cdot L^{-1}$) and cation/anion ratio (C/A) of winter precipitation, snowpack, snowmelt, soil solution, and streamwater during 55-d snowmelt period. Except for streamwater, HCO_3^- was determined on a subset of samples, and the cation/anion ratios are computed only for samples in this subset.

	C_B	Ca^{2+}	K^+	NH_4^+	H^+	NO_3^-	SO_4^{2-}	Cl^-	HCO_3^-	C/A
Precipitation	73.5	51.0	2.4	12.8	24.6	32.6	51.4	10.1	3.0	1.14
Snowpack	23.4	14.9	1.6	11.8	20.0	17.0	18.3	6.6	8.0	1.10
Snowmelt	45.1	29.0	4.9	18.3	38.9	38.6	44.5	7.9	—	1.12
Soil solution (15 cm)	389.2	260.6	19.8	10.1	1.7	44.0	109.7	18.0	177.0	1.17
Soil solution (30 cm)	451.2	272.6	21.1	10.5	1.6	123.0	99.6	19.9	83.0	1.21
Stream water	907.7	715.8	5.2	0.5	0.0	10.0	100.4	16.5	591.0	1.26

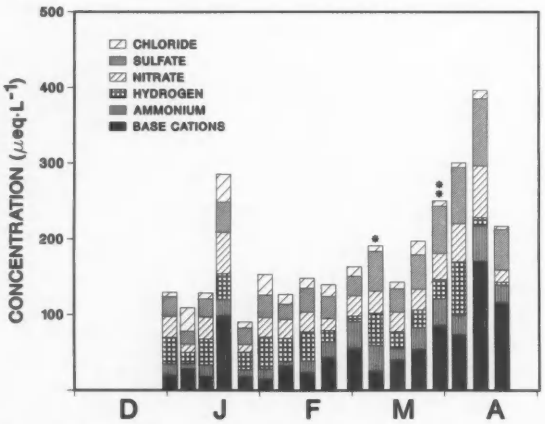

FIG. 7. Mean weekly precipitation ion concentrations for period of study. One asterisk, March 5 rain, two asterisks, March 24 rain.

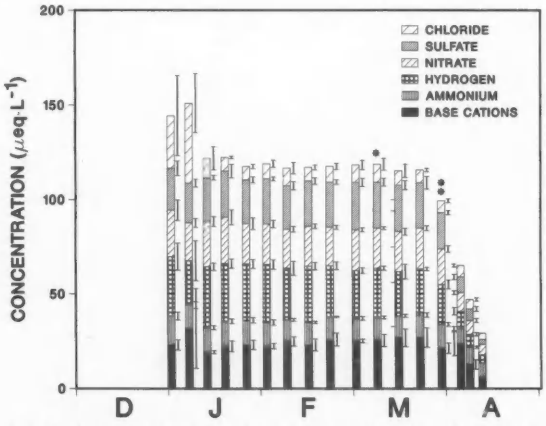

FIG. 8. Mean weekly snowpack ion concentrations for period of study. Brackets indicate one standard deviation. One asterisk, March 5 rain; two asterisks, March 24 rain.

TABLE 2. Weekly cation/anion ratio for NADP Station MI99 at Houghton, MI, watershed bulk precipitation collectors, and snowpack for period January 5 to April 19, 1988.

Week	NADP	Bulk	Snowpack
1/05	0.95	0.85	0.85
1/12	0.89	1.10	1.13
1/19	0.93	1.14	1.19
1/26	0.84	1.24	1.28
2/02	0.82	0.84	1.22
2/09	0.86	1.16	1.19
2/16	0.57	1.07	1.22
2/23	0.81	1.27	1.22
3/01	1.10	1.50	1.12
3/08	0.95	1.14	1.16
3/15	0.86	1.17	1.17
3/22	0.83	1.15	1.58
3/29	1.00	1.40	1.24
4/05	0.82	1.26	1.69
4/12	0.77	1.31	1.56
4/19	1.37	1.83	—
Mean	0.90	1.21	1.25
Minimum	0.57	0.84	0.85
Maximum	1.37	1.83	1.69

slightly preceded the rapid rise in streamwater discharge (Figs. 5 and 6). Maximum daily air temperatures were consistently above freezing and the snowpack remained isothermal. By the end of the first week in April, the mean SWE in the watershed had declined 10.9 cm, and that within the snow lysimeter plots by about 10 cm with a maximum daily SWE loss of 1.4 cm (Fig. 5). Over a period of 2.5 d the groundwater table rose >70 cm to the surface resulting in surface runoff (Fig. 6). Stream discharge increased from 19 to 126 $L \cdot s^{-1}$ exhibiting considerable diurnal fluctuation with daily peak flow occurring about 21:00 h. Widespread surface runoff over the forest floor continued for 8 d and, in general, ceased within 1 d following peak streamwater discharge (R. Stottlemyer, pers. observ.). The peak snowmelt rate and streamwater discharge occurred on April 10, during a period of rapidly declining SWE and following an additional 0.2 cm input of rain.

Precipitation Chemistry

Winter precipitation base cation (C_B) concentration was similar to that observed throughout the region (Foster and Nicolson 1988; Glass and Loucks 1986). Precipitation was acidic with a mean volume-weighted H^+ concentration of 25 $\mu eq \cdot L^{-1}$ (pH of 4.61) (Table 1; Fig. 7). Hydrogen, NO_3^-, and SO_4^{2-} concentrations were intermediate between those observed in Minnesota and the Lower Peninsula of Michigan (Glass and Loucks 1986; Verry 1983).

Bulk winter precipitation in the watershed had a mean cation/anion ratio of 1.21 (range 0.84 to 1.83) (Table 2). In both winter data sets, NADP station MI99 and watershed bulk precipitation, the highest ratios occurred toward the end of the permanent snow cover season. This suggests that dust inputs of additional base cations from the region may be present (Glass and Loucks 1986). There could also be seasonal variation in the input of

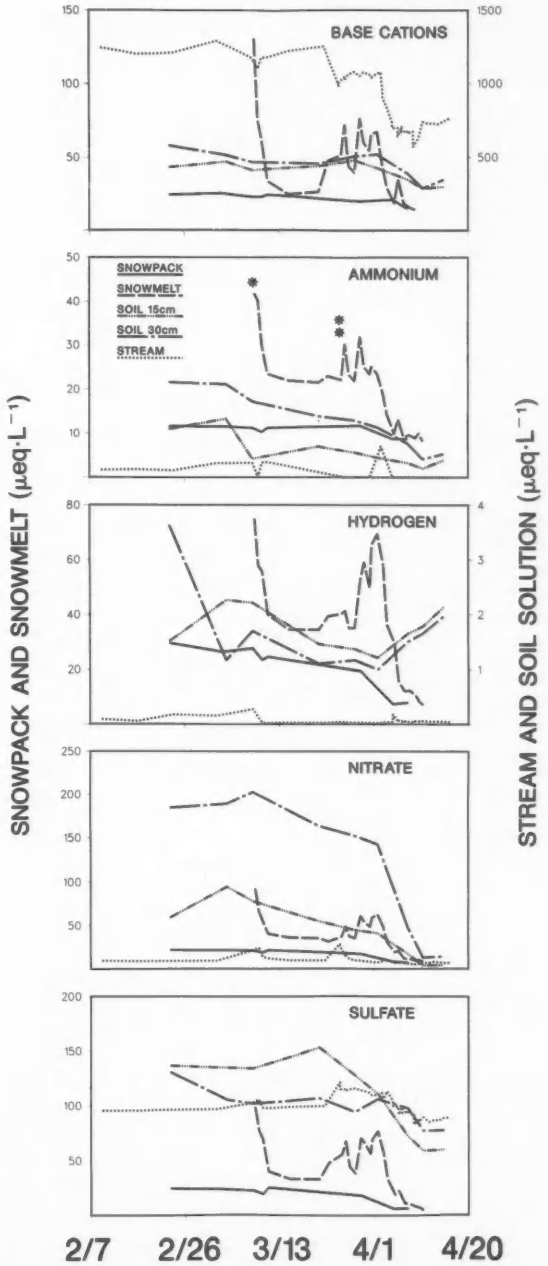

FIG. 9. Ion concentrations in snowpack, snowmelt, soil solution (15- and 30-cm depths), and streamwater during 55-d snowmelt period. One asterisk, March 5 rain; two asterisks, March 24 rain.

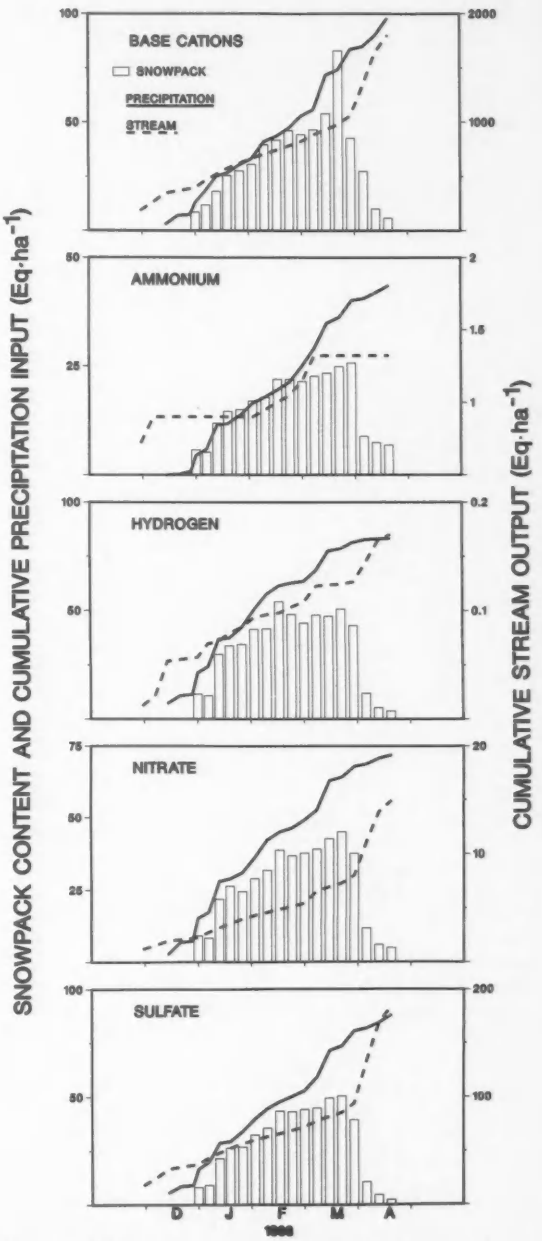

FIG. 10. Weekly average snowpack ionic load, mean cumulative precipitation input, and cumulative stream output.

organics such as acetate or formate, but these were not measured.

During the 8 yr of study in this watershed, we have found that, relative to mean annual precipitation concentration, C_B, NH_4^+, NO_3^-, and SO_4^{2-} concentrations decline with formation of regional snow cover (R. Stottlemyer, unpubl. data). Similar results have been found in other studies of the region (Glass and Loucks 1986). The reduction in C_B and NH_4^+ was likely related to snow covering open farmland in the region. Winter precipitation contained higher levels of NO_3^- relative to SO_4^{2-}. This could represent differences in snow and rain scavenging efficiencies for HNO_3 (Topol 1986) or a decline in the concentration of SO_4^{2-} relative to NO_3^-. Throughout the winter SO_4^{2-} gradually increased as a percent of total precip-

TABLE 3. Weekly percent snowpack moisture and ion loss for periods of snowmelt. Results are expressed as percentage of previous week's content and include weekly precipitation input. Where there was no net loss is indicated by "nc".

Week	SWE	Ca^{2+}	Mg^{2+}	Na^+	K^+	H^+	NH_4^+	NO_3^-	SO_4^{2-}	Cl^-
2/23	4	nc	1	nc	11	13	8	8	6	nc
3/01	6	19	18	10	nc	10	16	5	4	nc
3/08	1	4	4	5	nc	3	13	6	13	nc
3/29	10	61	55	23	nc	19	11	23	32	13
4/05	43	34	28	51	44	73	66	69	74	47
4/12	24	73	70	60	55	57	28	57	65	42

itation ion content. Increases in the relative concentration of SO_4^{2-} the week of March 22, and H^+ and SO_4^{2-} the weeks of March 6, and March 27, occurred with rain input (Figs. 2 and 7). The ratio of SO_4^{2-} to NO_3^- also increased during the season and was especially high with rain input. This trend was concurrent with a shift toward an increased frequency of southerly winds from low pressure systems (Stottlemyer 1987). Other investigators in the region have found similar trends (English et al. 1986; Semkin and Jeffries 1986).

Snowpack Chemistry

The dominant cation in the snowpack was H^+. Its concentration and load generally exceeded C_B until the beginning of snowmelt (Figs. 8–10). Sulfate was the dominant anion within the snowpack up to the final snowmelt period. With the late decrease in precipitation SO_4^{2-}/NO_3^- ratio and preferential SO_4^{2-} elution (Table 3), snowpack NO_3^- concentration and load exceeded SO_4^{2-} during the final 2 wk.

The mean cation/anion ratio in the snowpack was similar (mean = 1.25, range 0.85 to 1.69) to that observed in precipitation. As in precipitation, the highest ratios occurred later in the season (Table 2). The highest values occurred during maximum snowmelt when the ratio went from 1.17 the second week of March to 1.69 by the first week in April. This trend has been observed in other studies (Rascher et al. 1987). It suggests some increase in unmeasured organic anion inputs from debris such as budscales which blow into the snow from the surrounding forest or from dead grasses. It could also indicate increased cations from regional dust or road salt. There was no obvious weekly relationship between precipitation and snowpack cation/anion ratios suggesting that the trend in the snowpack originated independently of wet precipitation inputs.

Snowpack ion concentration approximated that of precipitation input until the end of February (Figs. 7 and 8) when the partial thaw (Fig. 5) contributed to snowpack ion loss. By the end of March precipitation ion concentrations were >2× that of the snowpack. At this time, daily freeze-thaw cycles, an isothermal snowpack (Fig. 4), and rain input rapidly reduced the ion concentration of the snowpack while precipitation concentrations were the highest of the winter season. The rain input during the first week of March, which resulted in some snowmelt and increase in stream water discharge, increased the snowpack SO_4^{2-}/NO_3^- ratio (equivalent basis) from 1.02 to 1.18. The ratio of SO_4^{2-}/H^+ and NO_3^-/H^+ also increased. Following this input, the ratio of SO_4^{2-}/NO_3^- and SO_4^{2-}/H^+ began a long steady decline. Conversely, the rain input during the week of March 24, which had a slightly higher SO_4^{2-}/NO_3^- ratio than the earlier rain, resulted in a sharp decline in total snowpack ion concentration and SO_4^{2-}/NO_3^- ratio. Relative to the March 5, input, this later rain had much more impact on snowpack ion concentration and content due to the presence of warm air temperatures and an isothermal snowpack.

Snowmelt and Stream Chemistry

The first snowmelt occurred the week of February 16–23 (Figs. 2 and 9; Table 3). There was a very small SWE loss, and a preferential release of K^+, H^+, NH_4^+, and NO_3^- (Table 3). This snowmelt period continued for another 2 wk during which there were pulses of all remaining ions.

While the release of snowpack ions in the initial snowmelt was small in terms of mass (Fig. 10), it resulted in concentrated input to the forest floor (Table 1; Fig. 9). Elevated snowmelt concentrations persisted 2 d for most ions. Snowmelt K^+ concentration increased the most relative to the snowpack concentration. This further suggested that K^+ leached from organic debris in the snowpack especially during melt. Potassium is easily leached from organic matter compared to ions, such as Ca^{2+}, incorporated as part of plant structural material (Hornbeck and Likens 1973). The rapidity of ion loss was likely promoted by the 0.9 cm rain input March 5. The increased rate of snowpack ion loss due to rain has been observed in other studies (Cadle et al. 1984). The rain input was especially high in H^+ and SO_4^{2-} (Fig. 7) which likely contributed to the high initial concentration of these ions in snowmelt.

Prior to snowmelt, streamwater C_B concentration was high and steady. Streamwater discharge was primarily groundwater high in C_B due to soil ion exchange and weathering (Fig. 9). C_B and HCO_3^- had much lower concentration in snowmelt than streamwater, and streamwater concentrations declined following the initial thaw. This along with the very small rate of increase in weekly ionic discharge from the watershed (Fig. 10; Table 4) indicated that the increase in streamwater discharge was due primarily to dilute meltwater and not increased groundwater which might result from meltwater exerting a piston action. The >200 $\mu eq \cdot L^{-1}$ C_B decline, due to dilution, and the concurrent gain of 25 $\mu eq \cdot L^{-1}$ in strong acid anions, NO_3^- and SO_4^{2-}, represented the maximum decrease in ANC during the initial melt.

For SO_4^{2-}, where the average snowmelt concentration was about one-half that of streamwater, there was a small increase in stream concentration concurrent with the initial snowpack loss. The SO_4^{2-} increase was only half that observed for NO_3^- even though the snowpack loads of NO_3^- and SO_4^{2-} were about equal (equivalent basis) this winter. The SO_4^{2-} increase probably occurred because a large pool of exchangeable SO_4^{2-} existed in surface soils which were at or near saturation (Galloway et al 1987; Stottlemyer and Hanson 1989). Also peak snowmelt concentrations were similar to lysimeter and stream SO_4^{2-} concentrations minimizing dilution during peak runoff.

TABLE 4. Weekly stream water and ion discharge during snowmelt (February 9 to April 19, 1988) expressed as a percentage of total winter discharge. Where there was no detectable ion concentration, discharge is indicated by "nc".

Week	Stream	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	C_B	H^{+}	NH_4^{+}	NO_3^{-}	SO_4^{2-}	Cl^{-}	HCO_3^{-}
2/23	2.2	2.5	3	3	1.8	2.6	4.6	11.5	2.1	2	2	3
3/01	2.1	2.7	3	3	2.6	2.8	4.0	23	2.2	2	3	3
3/08	3.7	4	4.7	4.3	2.1	4.3	12.6	41	9	9	3.6	6
3/15	4.3	3.3	3.6	3.5	2.2	3.3	0.8	nc	3	2.6	3.8	4
3/22	2.5	3.1	3.3	3.4	2.1	3.1	.7	nc	2.7	2.5	3.6	4
3/29	12.4	15.5	4.7	16	4.5	5.4	1.7	nc	5.4	22	17	6
4/05	21	20	17.4	19	31	19.6	15.5	nc	23.6	26.8	21.4	18
4/12	23	21	18.5	20.3	25.4	20.6	17	nc	21.4	23.3	18.5	18
4/19	11.2	11	10.5	8.7	10.1	10.8	5	nc	8	10	8	8

For ions in which the meltwater concentration exceeded that of streamwater, as NH_4^{+}, H^{+}, and NO_3^{-}, the initial thaw resulted in a small increase in stream H^{+} and NO_3^{-} concentration, but not NH_4^{+}. This suggested that NH_4^{+} might have been biologically taken up or oxidized to NO_3^{-}. However, expressed as a percentage of total winter discharge, NH_4^{+} discharge exceeded streamwater discharge for the period February 23, through March 8, (Table 4) after which concentrations fell below detection limits. The week of March 1–8, the percentage increase in NH_4^{+} discharge greatly exceeded that of streamwater discharge. Net NH_4^{+} input to the forest floor that week was 2.9 eq·ha^{-1} and stream discharge was 0.2 eq·ha^{-1}.

For H^{+}, the only week during which its increase in streamwater discharge clearly exceeded the increase in streamwater discharge was also March 1–8. The rather small streamwater H^{+} increase indicates most of it was exchanged for C_B in the forest soil and the input/output budget supports this. That week the net loss from the snowpack was 1.4 eq·ha^{-1}, but streamwater discharge was only 0.01 eq·ha^{-1}.

The increase in streamwater NO_3^{-} concentration was greatest relative to its snowmelt concentration, and during the week of March 1–8, the percent NO_3^{-} discharge exceeded that for streamwater discharge. Nitrate is normally strongly conserved in this watershed (Stottlemyer 1987). But during this week, the net snowpack loss of NO_3^{-} was 2.2 eq·ha^{-1} while stream discharge was 1.1 eq·ha^{-1}. The following week (March 15) the net loss from the snowpack was 6.5 eq·ha^{-1} but stream NO_3^{-} discharge was only 0.4 eq·ha^{-1}, a ratio common throughout most of the winter. These results for NH_4^{+}, H^{+}, and NO_3^{-} suggest that these early meltwaters were reaching the stream.

The initial snowmelt ionic loss was followed by 9 d of low volume dilute meltwater and little change in streamwater discharge. With initiation of the second and major snowmelt, beginning the week of March 20 (Fig. 5), all snowmelt ionic concentrations increased and exhibited similar patterns. Peak C_B and NH_4^{+} concentrations preceded the sustained high melt rates initiated about April 1. From March 21, to March 31, C_B, NH_4^{+}, H^{+}, NO_3^{-} and SO_4^{2-} concentrations in meltwater increased 52, 10, 24, 26, and 29 μeq·L^{-1}, respectively (Fig. 9) while streamwater C_B concentrations declined overall, NH_4^{+} concentration remained below detection, H^{+} increased a trace, NO_3^{-} about 18 and SO_4^{2-} 13 μeq·L^{-1}. Snowmelt H^{+}, NO_3^{-}, and SO_4^{2-} concentrations increased further on April 2, but resultant increases in streamwater concentration were less than observed earlier.

While streamwater discharge responded only slightly to the initial thaw, it increased sharply during the period of March 22, through April 5 (Fig. 2; Table 4). The percent discharge of Ca^{2+} increased relative to that of streamwater the week of March 22–29. This was the week of maximum net snowpack Ca^{2+} loss (42.5 eq·ha^{-1}) while streamwater Ca^{2+} discharge was 83 eq·ha^{-1} (Fig. 10). The peak discharge of Ca^{2+} (240 eq·ha^{-1}) occurred the week of April 12, while snowmelt and precipitation input that week was only 15.6 eq·ha^{-1}. This was during the last days of overland flow (Fig. 6), and along with the high HCO_3^{-} discharge suggests that meltwaters were exerting some piston action on groundwater increasing its relative contribution to stream discharge.

The percent K^{+} discharge exceeded that of streamwater from March 29, to April 12, which was also the period of maximum K^{+} loss from the watershed. K^{+} input to the forest floor those 2 wk was 2.7 eq·ha^{-1} while discharge was 4.5 eq·ha^{-1}.

The only week SO_4^{2-} discharge increased relative to streamwater was March 31–April 5 (Table 4). This was the week of maximum snowpack SO_4^{2-} loss (74% or 28.5 eq·ha^{-1}) and the initiation of overland flow (Fig. 6). Precipitation input that week was 1.3 eq·ha^{-1} and stream discharge 40.5 eq·ha^{-1}. The second highest weekly SO_4^{2-} discharge occurred the following week when the net snowpack SO_4^{2-} loss was 8.7 eq·ha^{-1} and streamwater discharge was 8.6 eq·ha^{-1}.

For those ions with higher concentrations in snowmelt than streamwater, much less of the ion load released during this final period of snowmelt reached the stream. The peak NH_4^{+} loss in snowmelt occurred during the week ending April 5, when the snowpack lost 66% of its NH_4^{+} load (17 eq·ha^{-1}) but streamwater NH_4^{+} remained below detection levels. The peak net snowpack H^{+} loss (33 eq·ha^{-1} or 73%) occurred during the week ending April 15, but stream discharge was only 0.02 eq·ha^{-1}. Net NO_3^{-} snowpack loss peaked (27 eq·ha^{-1} or 69%) the week ending April 5, and the percent NO_3^{-} discharge exceeded streamwater discharge. However, streamwater discharge was only 3 eq·ha^{-1} (Fig. 10, Table 4).

Soil Solution and Stream Chemistry

Passage of snowmelt through the forest floor, as measured by tension lysimeters at the 15 cm soil depth (A/E horizon), resulted in considerable modification of its chemistry (Table 1; Fig. 9). The cation/anion ratios were higher indicating the increased importance of organic anions (about 15% anion concentration at 15 cm and 25% at 30 cm (Hanson 1986)). The dominant ions in snowmelt were H^{+}, SO_4^{2-}, and NO_3^{-}, but in the shallow soil lysimeters Ca^{2+}, HCO_3^{-}, SO_4^{2-}, and organic acids (estimated from cation/anion ratio) were dominant while NH_4^{+} and H^{+} were reduced to 55 and 4% of the snowmelt concentration.

There was further modification of meltwater chemistry in deeper soils (30 cm depth, Bhs soil horizon) where Ca^{2+}, NO_3^{-}

and organic acids were dominant. The increase in Ca^{2+} was due to incresed soil depth, weathering of carbonate minerals, and ion removal from soil exchange sites (Hanson 1986). Except during the initial thaw and at the end of the snowmelt period, NO_3^- concentrations were significantly higher ($P < 0.05$) at the 30 cm soil depth compared with the 15-cm depth (Fig. 9). In an earlier 18 mo study in this watershed (Hanson 1986), four mineral soil horizons (A/E, Bhs, Bsl, and BC) were sampled by lysimeters, and the mean annual NO_3^- concentration in soil solution was also higher in the Bhs. However, the highest mean NO_3^- concentration in that study was 41 $\mu eq \cdot L^{-1}$ in zero-tension lysimeters just beneath the forest litter layer. This suggests that some nitrification occurs throughout the winter aided by the above-freezing soil temperatures, and that the very slow sustained snowmelt resulting from thawed soils may have moved the mineralized nitrogen to surface inorganic soil horizons where it was not taken up due to low biological activity.

Compared with lysimeter concentrations, C_B, HCO_3^- and estimated organic anion concentrations further increased in streamwater, but K^+, H^+, NH_4^+ and NO_3^- were markedly reduced. This was further evidence of the importance of groundwater contributions to C_B and HCO_3^- concentrations in streamwater and the strong watershed retention of the latter ions (Stottlemyer 1987).

With initiation of the second thaw, the groundwater table rapidly rose 40 cm at the monitoring well or into the Bhs horizon. Five days later it began another sharp rise to the soil surface resulting in 8 d of overland flow (Fig. 6). For those ions with much lower concentrations in snowmelt than streamwater, as C_B, the rapid rise in groundwater table, beginning on March 24, was accompanied by a sharp decline in streamwater C_B concentration but a continued increase in lysimeter concentrations (Figs. 6 and 9). While C_B concentration in meltwaters began to increase several days before the goundwater height increase, the net effect was still one of streamwater dilution decreasing the ANC by 260 $\mu eq \cdot L^{-1}$. These results again suggest that the soil solution was experiencing some influence from the steady release of snowpack moisture prior to the March thaws, and that the meltwaters from the March thaws did not penetrate very deeply into mineral soils but moved laterally through near-surface macropores as suggested by others (Driscoll et al. 1987).

As with C_B concentration, SO_4^{2-} concentration in meltwater during the second thaw also began to increase several days before the increase in groundwater height. The highest streamwater SO_4^{2-} concentration was concurrent with the second increase in streamwater discharge which peaked March 25 (Fig. 6), a rapid increase in goundwater height to about 50 cm, and a sharp increase in snowmelt SO_4^{2-} concentation. Sometime during the week of March 22–29, the SO_4^{2-} concentration in lysimeters began to decline especially at the 15-cm depth. Again this suggests rapid initial movement of meltwater and SO_4^{2-} to the stream through near-surface soil macropores prior to late March.

For those ions with meltwater concentrations higher than in streamwater, as NO_3^-, the second and highest NO_3^- pulse reached the stream before meltwater NO_3^- concentration increased, and it was concurrent with the rapid rise in groundwater height and streamwater discharge. This suggests that the initial meltwaters of this second thaw, while showing no increase in NO_3^- concentration, picked up mobile NO_3^- from the surface organic and inorganic horizons as the water rapidly passed through macropores to the stream. Increases in streamwater acid anions, NO_3^- and SO_4^{2-}, at this time further reduced streamwater ANC by 48 $\mu eq \cdot L^{-1}$.

Additional evidence of this transport path for meltwater to the stream was provided by examining the ion pair correlations in shallow lysimeter soil solution during both the initial and second melt periods. Essentially, these remained unchanged with the only high correlation being between C_B and SO_4^{2-}. This suggests that even during much of the second melt period, meltwater did not significantly alter shallow soil solution chemistry.

When overland flow occurred, beginning the first week of April (Fig. 6), streamwater C_B concentration declined 475 $\mu eq \cdot L^{-1}$ due to dilution. By late March C_B concentration in the 15-cm lysimeters began to decline, and by early April it started to decline in the 30-cm deep lysimeters. This was further evidence supporting the hypothesis that meltwaters were then exerting a piston action on deeper C_B-rich groundwater accounting for the peak C_B stream discharge the week of April 5–12.

During the overland runoff, lysimeter NO_3^- concentration declined sharply while its stream concentration returned to premelt levels. Stream SO_4^{2-} concentration began to decline, and was very similar to lysimeter concentrations. By the end of the melt period streamwater SO_4^{2-}/NO_3^- ratios began to increase above their premelt levels likely due to deeper soil water contributions of SO_4^{2-} and/or the increasing biological uptake of NO_3^-. The small stream pulse principally of H^+ with some NO_3^- and SO_4^{2-} on April 5, likely reflected that week's rain input on saturated soils.

Discussion

Precipitation and Hydrology

The increase in precipitation amount with elevation was unexpected especially for a watershed with such low elevation and only a small (185 m) elevation change. This also provides an opportunity for increased ionic deposition with elevation. Upper portions of watersheds are potentially more sensitive to such iputs because they exhibit sharper runoff peaks, higher storm levels, and shorter water residence times which reduce the opportunity for solute incorporation by soil exchange or biological uptake (Likens et al. 1977).

The occurrence of midwinter thaws, especially coupled with unfrozen soils, appears to be an important factor in determining the extent of subsequent near-surface and surface lateral flow. Meltwater from initial thaws largely remained within the watershed and elevated the groundwater height reducing the soil water storage capacity and setting the stage for sharper subsequent snowmelt runoff. This has also been found in the Adirondacks (Newton and Driscoll 1987). This process is especially important in watersheds with relatively shallow depth to bedrock or with shallow cemented impervious layers, as ortstein, because it can considerably reduce the residence time of meltwater prior to its reaching the stream or lake. The occurrence of such an impervious layer is pervasive in our watershed and throughout major portions of the region (McKeague and Wang 1980).

About 45% of the winter period's streamwater discharge occurred during the time we observed surface runoff of snowmelt. While we have no direct measurement of the quantity of this surface and near-surface soil lateral water movement, weekly streamwater discharge during this period was twice that

which occurred in the week prior to and following surface runoff (Table 4). This suggests that up to 20% of the seasonal streamwater discharge could have occurred as surface and near-surface soil lateral flow. During surface runoff, daily streamwater discharge fluctuated greatly with increases of up to 100% occurring from the low at 09:00 h to the peak at about 21:00 h.

Snowmelt and Stream Chemistry

If one defines a snowmelt "pulse" as a period of time when the increase in ionic loss exceeds that of SWE, all ions showed such a condition at one time or another during the early and late snowmelt periods. SO_4^{2-} did not show a pronounced early pulse which has generally been the finding in other studies (Cadle et al. 1984; Davies et al. 1982; Johannessen and Henriksen 1978; Semkin and Jeffries 1986). The largest relative differences in snowmelt solute and SWE losses were the divalent base cations both at the beginning and end of the peak snowmelt period. For anions, SO_4^{2-} showed the largest pulse in the middle and end of the peak snowmelt period.

The effect of a snowmelt ionic pulse on streamwater chemistry appears to depend on whether it occurs early or late in the snowmelt period. For example, about 10% of a relatively small (2.9 eq·ha^{-1}) snowpack NH_4^+ loss the week ending March 8 resulted in the most pronounced increase in NH_4^+ discharge relative to streamwater increase. Yet there was little or no change in streamwater NH_4^+ discharge following the largest 1-wk NH_4^+ loss from the snowpack (17 eq·ha^{-1}) during the week ending April 5. Likely much of the NH_4^+ released during peak snowmelt was oxidized to NO_3^- for this was one of two weeks that the percent NO_3^- discharge increased relative to streamwater. The similar but less pronounced seasonal trend in H^+ likely reflects improved late season conditions for exchange of snowmelt H^+ with increased biological activity and temperature. However, the snowmelt H^+ release the week ending March 8, which resulted in the only streamwater H^+ pulse observed, could have been due in part to winter accumulations of H^+ in forest soils.

The major snowmelt NO_3^- pulses occurred during the same time periods as did maximum stream NO_3^- discharge. The initial snowmelt NO_3^- pulse, the week of February 23, never reached the stream. Fifty percent of the second snowmelt pulse, the week of March 8, was lost in stream discharge. This loss also could have included some NO_3^- accumulated in the soil through nitrification and earlier snowmelt. However, during peak snowmelt NO_3^- loss the week ending April 8, stream NO_3^- discharge was reduced to 11% of inputs to the forest floor. This reduced loss was likely due to increased ecosystem uptake with the advancing season.

The large SO_4^{2-} load in the snowpack and its release in snowmelt had less effect on change in streamwater chemistry than might be expected. The enriched pre-melt streamwater SO_4^{2-} concentration minimized the effect of snowmelt inputs. Conversely, premelt streamwater NO_3^- concentrations were very low relative to NO_3^- concentration in snowmelt. Thus during the initial snowmelt in early March when SO_4^{2-} was being released more rapidly than NO_3^- from the snowpack, the SO_4^{2-}/NO_3^- ratio increased in meltwater but sharply declined in streamwater. This was due to the relative gain in streamwater NO_3^- concentration.

Our results again point out the potential importance of surface runoff and near-surface macropores in promoting rapid movement of meltwaters to the stream. Further evidence of rapid meltwater transport to the stream can be found by examining correlations between ion pairs in snowmelt and streamwater during both the initial and second melt periods. All ion pairs (H^+ to NO_3^-, H^+ to SO_4^{2-}, SO_4^{2-} to NO_3^-, and C_B to SO_4^{2-}) in snowmelt were highly correlated both during and following the initial and second melt periods. However, during and following the initial melt, streamwater showed high correlation only between C_B and SO_4^{2-} ($r^2 = 0.62$, $p < 0.05$) and SO_4^{2-} to NO_3^- ($r^2 = 0.96$, $p < 0.01$). During the second melt period, streamwater showed a high correlation between C_B and SO_4^{2-}, H^+ and NO_3^- ($r^2 = 0.77$, $p < 0.001$) and H^+ and SO_4^{2-} ($r^2 = 0.34$, $p < 0.05$). This suggests, especially during much of the second melt, that meltwater had much reduced contact with mineral soil. This would have been the result of reduced residence time and/or increased overland flow.

Even though the stream's dominant anion was HCO_3^-, its responses to snowmelt ionic inputs, though reduced in magnitude, were similar to those observed in more sensitive streams (Rascher et al. 1987). The most pronounced decrease in streamwater ANC occurred with overland flow of meltwater and was largely attributable to dilution. However, while the processes of ecosystem response to snowmelt may be similar among sites, the fact that extensive areas of Michigan's Upper Peninsula are dominated by alkaline glacial till (Stottlemyer 1982) indicates that the high snowpack loads of H^+ will likely have little direct impact on surface water chemistry. Possible exceptions to this general statement would be those portions of the region dominated by glacial outwash sands (Linthurst et al. 1986) or with shallow soils underlined by Precambrian granites (Jeffries et al. 1979).

Conclusions

Results of this study show that there is a small but steady snowpack loss of many ions during the entire winter due likely to unfrozen soils. Midwinter thaws, especially when accompanied by rain, result in major change in snowpack chemistry, the chemistry of snowmelt, and a reduction in snowpack ionic load.

Preferential snowpack elution of K^+, NH_4^+, and H^+ occurred during the earliest thaw, divalent base cations during the second thaw, and Ca^{2+} and SO_4^{2-} during peak snowmelt. These snowmelt pulses were generally reflected as pulses in streamwater ionic discharge.

There was some evidence that early releases of H^+ and NO_3^- in snowmelt were added to when meltwaters passed through the surface forest soils. These additions likely came from the products of over-winter mineralization/nitrification.

For those ions with snowpack concentrations greater than in streamwater, H^+, NH_4^+, and NO_3^-, the relative importance of snowmelt ion pulses on streamwater chemistry appeared dependent upon the time of snowmelt release. In midwinter, snowmelt pulses, while relatively small in term of mass, had a much greater relative effect on changing surface water chemistry than did snowmelt pulses of much larger mass which occurred late in the snowmelt season.

The SWE, its solute load, and the duration of the snowpack were much below average the winter of 1987–88, and this restricts application of the findings in developing more general hypotheses on snowpack processes and their relationship to soil solution and surface water chemistry of the region.

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MULTIFAN a Likelihood-Based Method for Estimating Growth Parameters and Age Composition from Multiple Length Frequency Data Sets Illustrated using Data for Southern Bluefin Tuna (*Thunnus maccoyii*)

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Fournier, D. A., J. R. Sibert, J. Majkowski, and J. Hampton. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). Can. J. Fish. Aquat. Sci. 47: 301–317.

We present a method for simultaneously analyzing multiple length frequency data sets. The method utilizes a robust likelihood-based estimation procedure that provides an objective criterion for hypothesis testing. The method is applied to length frequency data from southern bluefin tuna (*Thunnus maccoyii*) for which independent estimates of growth parameters based on tag return data are available. The estimates of the growth parameters from the new method were found to be in substantial agreement with the values previously obtained for these parameters. The strength of the likelihood approach is demonstrated by discriminating between alternative structural hypotheses for describing the data. The ability to simultaneously analyze multiple samples permits the method to exploit the extra information not available when analyzing samples one by one. The computer program maintains a database of fits to the data which enable the user to organize the results of the analysis. Graphical displays permit the user to view any of the fits, and an interactive graphics routine aids the user to find good initial parameter estimates.

Les auteurs présentent une méthode permettant d'analyser simultanément plusieurs échantillons de fréquence de tailles. Elle utilize une procédure d'estimation robust, bassé sur la theorie du maximum de vraisemblance qui fournit un critère objectif de test des hypothèses de départ. La méthode est appliquée aux données de fréquence de tailles du thon rouge du sud, pour lequel des estimations de la croissance à partir de marquage sont disponibles. Les estimations de paramètres décrivant la croissance, calculées par le logiciel, concordent bien avec les valeurs obtenues préalablement pour ces paramètres. La puissance de l'approche par maximum de vraisemblance permet de faire des choix entre les différentes hypothèses de structure devant décrire le données. La capabilité de traiter simultanément plusieurs échantillons permet d'exploiter des informations supplémentaires non disponibles lorsque les échantillons sont analysés séparément. Le logiciel tient à jour une base de données des ajustements qui permet à l'utilzateur d'organizer les résultats de l'analyse. Les restitutions graphiques rendent possible la visualisation des ajustements, et un procédure graphique interactive permet à l'utilizateur de trouver les bonnes estimations initiales des paramètres.

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Modern computer-based methods for estimating the parameters that describe growth and age composition from fisheries length frequency data originate with the work of Hasselblad (1966) who developed a method for separating a finite mixture of normal distributions by employing a maximum likelihood estimation procedure. Macdonald and Pitcher (1979) showed how variations of Hasselblad's (1986) technique could be applied to fisheries length frequency data. Schnute and Fournier (1980) and Fournier and Breen (1983) introduced additional structure based on biological considerations into Hasselblad's method. This produced a method for simultaneously estimating the parameters describing growth, age composition, and total mortality from a single length frequency data set.

It has long been recognized that the reliability of parameter estimates derived from a single data set of typical fisheries length frequency data is limited. For example, Fournier and Breen (1983) conclude from the analysis of simulated data that estimates of von Bertlanaffy K tend to be too low when derived from a single data set. Better parameter estimates can be obtained by simultaneously analyzing several length frequency data sets obtained at several different times from a fish population.

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Another handicap imposed by simply analyzing a single data set is the inability of the model to estimate the number of significant age-classes represented in the data. Rosenberg and Beddington (1987) reported that significant bias in the parameters describing growth occurred when the number of age-classes was underestimated. The simultaneous analysis of several length frequency data set holds the promise of more accurate estimation of the number of significant age-classes represented in the data.

An early attempt at such a method is the ELEFAN system described in Pauly (1987). While the ELEFAN system has been widely used, the method is based on ad hoc estimation procedures. (see Hampton and Majkowski 1986a; and Rosenberg and Beddington 1987 for discussions of the applicability and reliability of ELEFAN).

A likelihood-based method extending the methods of Schnute and Fournier and Fournier and Breen to simultaneously analyze several length frequency data sets would be an important advance. Likelihood methods utilize the large body of existing statistical theory for interpreting the resulting parameter estimates as well as providing an integrated overall approach for including and evaluating different structural hypotheses into the model in a consistent fashion. The present paper describes such a procedure, referred to as the MULTIFAN model.

Sparre (1987) described a method for simultaneously analyzing several length frequency data sets. His method employs a minimum χ^2 estimator which is asymptotically equivalent to Hasselblad's maximum likelihood estimator. A problem associated with the maximum likelihood estimator of Hasselblad or the minimum χ^2 estimator of Sparre is their lack of robustness. Nonrobust estimation procedures are too sensitive to deviations from the model's hypotheses. Another problem associated with these estimators is that often the model simply does not fit the data as well as it would if the assumptions underlying the adoption of either of these estimation procedures were valid. This renders the results of hypothesis tests based on the values of either of these statistics unreliable.

We shall introduce a statistical model which can adequately describe the length frequency data and a corresponding robust maximum likelihood estimation procedure. This estimation procedure will serve as a basis for carrying out tests to compare the structural hypotheses underlying various models. While we concur with Sparre that the analysis of length-frequency data will probably never be entirely objective, we feel that the use of this new estimation method reduces the subjectivity of the analysis, particularly when attempting to determine the number of significant age-classes represented in the data.

One difficulty often associated with applying nonlinear statistical models is the organization and interpretation of analytical results which are produced by many alternative attempts to fit the data. The MULTIFAN procedure organizes the results of the analysis and presents them in convenient graphical and tabular forms for ready interpretation. The MULTIFAN procedure also provides interactive graphical presentations which permit the user to pick initial parameter estimates and to incorporate obvious features of the data into the structural hypotheses of the model.

To illustrate the performance of MULTIFAN, we have applied it to length frequency data sets from southern bluefin tuna (*Thunnus maccoyii*). This species provides excellent data for testing the method. There is a long time series of data available which extends over many years and includes data sets from all seasons of the year. The nature of the fishery changed during this time period to include younger fish. The effect of selecting data from different periods on estimates of the growth parameters can be examined. By splitting the data into smaller subsets, the performance of the model on a shorter series of data more typical of developing fisheries can be evaluated. The long time series also makes it possible to test for the existence of size selectivity in the recruitment of the first age-class. Serious bias in the estimation of growth parameters can occur if such size selectivity is not detected and included in the model parameterization. Finally, estimates of growth rates based on independent tagging data are available for comparison with the results of the new method.

Before the development of the method presented in this paper, the catches by year and age-class for southern bluefin tuna were being routinely estimated from length frequencies by calculating ages from lengths on the basis of a deterministic age–length relationship (see Majkowski and Hampton 1983a, b). The major weakness of this method is that it does not take into account the variability of lengths at a given age. The procedure presented in this paper has the potential to significantly improve the estimates of the age composition of the catch of southern bluefin tuna. This progress is very desirable from the view point of stock assessment and, consequently, fisheries management.

Model Formulation

The following notation is introduced to describe the MULTIFAN model:

- i Subscript indexing the length frequency intervals.
- j Subscript indexing the age-classes.
- α Subscript indexing the length frequency data sets.
- N_J Number of age-classes present in the data sets.
- N_A Number of length frequency data sets.
- N_I Number of length intervals in each length frequency data set.
- S_α Number of fish in the αth length frequency data set.
- $f_{i\alpha}$ Number of fish whose lengths lie in the ith length interval in the αth length frequency data set.
- $p_{j\alpha}$ Proportion of age-class j fish in the αth length frequency data set.
- $q_{ij\alpha}$ Probability that an age-class j fish picked at random from the fish which were sampled to get the αth length frequency data set has a length lying in length interval i.
- $Q_{i\alpha}$ Probability that a fish picked at random from the fish which composed the αth length frequency data set has a length lying in length interval i.
- $\tilde{Q}_{i\alpha}$ Proportion of fish in the αth length frequency data set having a length lying in length interval i.
- $\mu_{j\alpha}$ Mean length of the age-class j fish in the αth length frequency data set.
- $\sigma_{j\alpha}$ Standard deviation of the length distribution of the age-class j fish in the αth length frequency data set.
- x_i Midpoint of the ith length frequency interval.
- ω Width of the length frequency intervals.
- L_1 Mean length of the first age-class on the von Bertalanffy curve in month 1.
- L_{N_J} Mean length of the last age-class on the von Bertalanffy curve in month 1.
- K Von Bertalanffy K parameter.
- ρ Brody growth coefficient ($K = -\ln(\rho)$).
- λ_1, λ_2 Parameters determining the standard deviations $\sigma_{j\alpha}$.

τ_α Parameters determining the overall variance of the sampling errors in the αth length frequency data set.

$\xi_{i\alpha}$ Parameters determining the relative variances of the sampling errors within the αth length frequency data set.

δ Parameter determining the variance of the sampling errors in all the length frequency data set.

b_1 Parameter determining the amount of size selectivity for the first age-class.

Assume that the $Q_{i\alpha}$ depend on a set $\Theta = (\theta_1,\ldots,\theta_r)$ of parameters. The exact form and number of the parameters depends on the specific model formulation which w do not wish to specify at this stage. We denote this dependence by writing $Q_{i\alpha}(\Theta)$.

If the length frequency data arose from random samples where the probability of each fish in the αth data set having a length lying in length interval i is $Q_{i\alpha}(\Theta)$, the probability of obtaining the observed length frequencies $f_{i\alpha}$ is equal to a constant times the expression

$$(1.1)\quad \prod_{\alpha=1}^{N_A}\prod_{i=1}^{N_I} Q_{i\alpha}(\Theta)^{f_{i\alpha}}.$$

The maximum likelihood estimates for the parameters Θ are found by maximizing (1.1) or equivalently by maximizing the log-likelihood function (1.2) with respect to these parameters.

$$(1.2)\quad \sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_I} f_{i\alpha}\ln(Q_{i\alpha}(\Theta)).$$

The A statistic, (1.3), introduced for length frequency analysis in Schnute and Fournier (1980) is more convenient than the log-likelihood function,

$$(1.3)\quad A = -2\sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_I} f_{i\alpha}\ln(Q_{i\alpha}(\Theta)/\tilde{Q}_{i\alpha}),$$

where $\tilde{Q}_{i\alpha}$ is the proportion of fish in the αth data set whose lengths lie in length interval i. The advantage of (1.3) over (1.2) is that under the hypothesis that the model is correct, (1.3) is asymptotically distributed as a χ^2 random variable with $N_A N_I$ − (number of parameters in the model) degrees of freedom. This makes it possible for the user to get a quick idea of how well the model is fitting the data. Minimizing the A statistic is equivalent to maximizing the log-likelihood function.

Maximum likelihood estimation using the log-likelihood function for a multinomial distribution (1.2) for estimating the parameters for a mixture of normal distributions was introduced by Hasselblad (1966) and has generally been shown to produce good parameter estimates. However, this estimation procedure has serious drawbacks when used for significance testing (likelihood-ratio tests) and for estimating the covariance matrix of the parameter estimates. The reason for this is that the model seldom fits the data as well as one would expect for a multinomial distribution with a random sample of the size used. This can be due to systematic departures from randomness in the sampling scheme as well as departures from the assumptions made about the distribution of the length-at-age of the fish. For a multinomial distribution with a sample of size n if the probability of observing fish whose lengths lie in a given length interval is q, and $\tilde{q}$ is the actual proportion observed, the variance of the random variable $\tilde{q}$ is equal to $q(1-q)/n$. The variance of $\tilde{q}$ is determined by the sample size alone.

Significance tests such as the likelihood-ratio test are valid only if the statistical model adequately describes the data. Since significance tests form an important part of length frequency analysis (they are used to determine how many age-classes are represented in the mixture), this is a severe limitation. To overcome this problem we shall introduce an alternative statistical model which does not assume that the variance of the difference between the expected and observed length-frequencies decreases in a predictable fashion as the sample size increases. Rather it allows the fit between the observed and predicted data to determine the variance of these random differences. This approach is similar to that used in linear regression models, where the residuals determine the estimated variance of the random components of the model. We shall combine the linear regression approach with techniques from robust statistical estimation theory to formulate a robust statistical estimation procedure which can adequately describe the process of interest and which will provide a basis for hypothesis testing.

Robust Estimation

The method of maximum likelihood has long enjoyed a preeminent position among statistical estimation procedures. Recently it has been realized that, although maximum likelihood estimates have good properties when the model's assumptions are satisfied, their performance can degrade rapidly when departures from the model's assumptions occur. The property of a statistical estimator which permits it to behave well over a range of deviations from the statistical assumptions is called robustness.

In real applications, robustness considerations often are more important than the theoretical optimal properties of the conventional maximum likelihood estimates. Our goal in this paper is to retain the advantages of maximum likelihood estimation, but to incorporate into the model's structure the possibility of a few large deviations from the model's hypotheses and to construct a robust likelihood-based estimation scheme which can provide an adequate description of the data.

Two different types of deviations from a model's hypotheses can occur in length frequency analysis. A length may be recorded in a region where the model predicts that there is almost no probability of observing such a fish. An example is a fish whose length is much longer than that of any other fish. Such an observation may arise from an error in transcribing data or simply represent an unusual event. In any case, it may have an undue influence on the maximum likelihood estimates obtained by maximizing the expression (1.2). We shall call the occasional occurrence of an event of very low probability a type I deviation.

The other type of deviation occurs in a region where the probability of observing a fish length is high. In this case, the frequency observed in a length interval is either much higher or much lower than it should be considering the accuracy of the majority of the observations. This will be termed a type II deviation. Our goal is to make the model insensitive to a small number of type I or type II deviations.

If the $\tilde{Q}_{i\alpha}$ are derived from a random sample size S_α, they would be random variables with means $Q_{i\alpha}$ and variances $(1-Q_{i\alpha})\,Q_{i\alpha}/S_\alpha$. Set $\xi_{i\alpha} = (1-Q_{i\alpha})\,Q_{i\alpha}$. The $\xi_{i\alpha}$ determine the relative variances of the $\tilde{Q}_{i\alpha}$ within a sample while the S_α can be regarded as a scale factor determining the overall size of all the variances of $\tilde{Q}_{i\alpha}$ in a sample.

As $Q_{i\alpha}$ tends to zero, the corresponding $\xi_{i\alpha}$ tends to zero as well. This reflects the fact that for random sampling an event with very small probability will almost never occur. For real

world data, however, highly unlikely events seem to occur quite often. To render the model less sensitive to the occurrence of unlikely events, a lower bound is put on the relative variances of the $\tilde{Q}_{i\alpha}$. The scale factor S_α is replaced by a parameter τ_α to be estimated within the model.

We assume that the variance of the random variable $\tilde{Q}_{i\alpha}$ is equal to $(\xi_{i\alpha} + .1/N_l)\tau_\alpha^2$ where the τ_α are parameters to be estimated. The term $.1/N_l$ is included so that the expression for the relative variance does not tend to zero as the corresponding $Q_{i\alpha}$ tends to zero. This renders the model insensitive to type I deviations.

If the $\tilde{Q}_{i\alpha}$ were independent, normally distributed random variables, their likelihood function would have the form

$$(2.1)\quad \prod_{\alpha=1}^{N_A}\prod_{i=1}^{N_l}\left[\frac{1}{\sqrt{2\pi(\xi_{i\alpha}+.1/N_l)\tau_\alpha}} \times \exp\left\{-\frac{(\tilde{Q}_{i\alpha}-Q_{i\alpha})^2}{2(\xi_{i\alpha}+.1/N_l)\tau_\alpha^2}\right\}\right].$$

This likelihood function, based on a normal distribution, is too sensitive to large deviations from the expected value $Q_{i\alpha}$. It lacks robustness. To make (2.1) more robust, we assume that there is a small uniformly distributed contamination of the normal distribution. This will render the model insensitive to type II deviations. The likelihood function becomes

$$(2.2)\quad \prod_{\alpha=1}^{N_A}\prod_{i=1}^{N_l}\left[\frac{1}{\sqrt{2\pi(\xi_{i\alpha}+.1/N_l)\tau_\alpha} \times \left(\exp\left\{-\frac{(\tilde{Q}_{i\alpha}-Q_{i\alpha})^2}{2(\xi_{i\alpha}+.1/N_l)\tau_\alpha^2}\right\}+.01\right)}\right].$$

The reason for picking the value .01 in (2.2) is that for a normal distribution one usually begins to consider an observation to be a candidate for outlier status when it is about three standard deviations removed from the mean. For the moment let σ denote the standard deviation of a normally distributed random variable, and let $u = 3\sigma$. Then $\exp(-u^2/2\sigma^2) \approx 0.011$, so that the use of .01 in (2.2) ensures that the influence of observations on the parameter estimates decreases rapidly as their distance from the mean grows greater than three standard deviations. Taking the logarithm of (2.2) we obtain the log-likelihood function

$$-1/2\sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_l}\log_e(2\pi(\xi_{i\alpha}+.1/N_l))$$

$$(2.3)\quad -\sum_{\alpha=1}^{N_A}N_l\log_e(\tau_\alpha) + \sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_l}\log_e\left[\exp\left\{\frac{-(\tilde{Q}_{i\alpha}-Q_{i\alpha})^2}{2(\xi_{i\alpha}+.1/N_l)\tau_\alpha^2}\right\}+.01\right].$$

There are several possibilities for reparameterizing the τ_α which represent different assumptions about the relative accuracies of the observed length frequencies composing the different length frequency data sets. In this paper we have assumed that all samples are equally accurate. Let δ be a model parameter which determines the overall size of the variances in the sampling errors. The assumption that all samples are equally accurate is implemented by setting $\tau_\alpha = \delta$ for all α.

Expression (2.3) forms the basis for the robust likelihood-based estimation scheme we have adopted, that is, the parameters are estimated by maximizing expression (2.3). Of course the $\tilde{Q}_{i\alpha}$ are not independent, normally distributed random variables. For a multinomial distribution the random variables $\tilde{Q}_{i_1\alpha}$ and $\tilde{Q}_{i_2\alpha}$ are correlated with correlation equal to $-Q_{i_1\alpha}Q_{i_2\alpha}/S_\alpha$. This may give cause for asking whether minimizing (2.3) provides a good parameter estimation scheme for analyzing length frequency data. To motivate the use of (2.3), we shall show that it is essentially a "robustified" minimum χ^2 estimator. Consider expression (2.1). Since in general less than say 30% of the fish lie in any one length frequency interval, $\xi_{i\alpha}$ is approximately equal to $Q_{i\alpha}$. Assuming for the moment that the τ_α are fixed, maximizing the expression (2.1) is the same as minimizing the sum

$$(2.4)\quad \sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_l}\frac{(\tilde{Q}_{i\alpha}-Q_{i\alpha})^2}{(\xi_{i\alpha}+.1/N_l)\tau_\alpha^2},$$

which is almost the same as

$$(2.5)\quad \sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_l}\frac{(\tilde{Q}_{i\alpha}-Q_{i\alpha})^2}{(Q_{i\alpha})\tau_\alpha^2}$$

Now setting τ_α^2 equal to $1/S_\alpha$ in (2.5) yields

$$(2.6)\quad \sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_l}\frac{(S_\alpha\tilde{Q}_{i\alpha}-S_\alpha Q_{i\alpha})^2}{(S_\alpha Q_{i\alpha})}.$$

Expression (2.6) is the minimum χ^2 statistic. Thus, (2.3) is approximately equal to a self-scaling robustified minimum χ^2 statistic.

Main Assumptions of the Model

At this point, there are far too many independent parameters in the model to obtain useful parameter estimates. Most of the model structure involves some biological assumptions which are made to reduce the number of independent parameters. The main structural assumptions are:

(1) The lengths of the fish in each age class are normally distributed around their mean length (see 3.1).
(2) The mean lengths at age lie on (or near) a von Bertalanffy growth curve (see 3.3).
(3) The standard deviations of the actual lengths about the mean length at age are a simple function of the mean length at age (see 3.4).

If the lengths of the age class j fish in the αth length frequency data set are normally distributed around their mean $\mu_{j\alpha}$ with standard deviations $\sigma_{j\alpha}$, $q_{ij\alpha}$ can be expressed in terms of $\mu_{j\alpha}$ and $\sigma_{j\alpha}$ by

$$(3.1)\quad q_{ij\alpha}(\mu_{j\alpha},\sigma_{j\alpha}) = \frac{1}{\sqrt{2\pi}\,\sigma_{j\alpha}}\int_{x_i-w/2}^{x_i+w/2}\exp\left\{\frac{-(x-\mu_{j\alpha})^2}{2\sigma_{j\alpha}^2}\right\}dx.$$

As long as $\sigma_{j\alpha} > w$ the integral can be approximated sufficiently well by setting

$$(3.2)\quad q_{ij\alpha}(\mu_{j\alpha},\sigma_{j\alpha}) = \frac{w}{\sqrt{2\pi}\,\sigma_{j\alpha}}\exp\left\{\frac{-(x_i-\mu_{j\alpha})^2}{2\sigma_{j\alpha}^2}\right\}$$

This aproximation has been used in the model.

Now assume that the mean lengths $\mu_{j\alpha}$ lie on a von Bertalanffy curve so that

$$(3.3)\quad \mu_{j\alpha} = L_1 + (L_{N_J} - L_1)\left(\frac{1-\rho^{j+(m(\alpha)-1)/12}}{1-\rho^{N_J}}\right),$$

where L_1, the mean length of the first age-class, L_{N_J}, the mean length of the last age-class, and ρ, the Brody growth coefficient, are the three parameters which determine the form of the von Bertalanffy curve, and $m(\alpha)-1$ is the number of months after the presumed birth month of the fish in the αth length frequency data set. This parameterization of the von Bertalanffy growth curve is from Schnute and Fournier (1980).

The parameterization for the standard deviations $\sigma_{j\alpha}$ as a simple function of length involving two parameters λ_1 and λ_2 is given by

$$(3.4)\quad \sigma_{j\alpha} = \lambda_1 \exp\left\{\lambda_2\left[-1+2\left(\frac{1-\rho^{j+(m(\alpha)-1)/12}}{1-\rho^{N_J}}\right)\right]\right\}$$

where the term enclosed in square brackets expresses the length dependency of the standard deviations independently of the numerical values of the parameters L_1 and L_{N_J} (cf. 3.3). The two coefficients, λ_1 and λ_2, transform the rescaled length to the standard deviations. λ_1 determines the magnitude of the standard deviations, and λ_2 determines the length-dependent trend in the standard deviations. If $\lambda_2 = 0$, the standard deviations are length-independent.

The parameters p_i, L_1, L_{N_J}, K, λ_1, λ_2 and δ for $1 \leq j \leq N_J$ form the fundamental set of parameters in terms of which all the other parameters can be expressed and log-likelihood function (2.3) can be calculated. (If the relative accuracies of the length frequency data set are to be estimated, then the τ_α are independent model parameters instead of δ.) Note that the $Q_{i\alpha}$ satisfy the relationship

$$(3.5)\quad Q_{i\alpha} = \sum_{j=1}^{N_J} p_{j\alpha} q_{ij\alpha}.$$

The steps in the calculation of the model parameters are:
(1) Calculate the $\sigma_{j\alpha}$ from (3.4) using the fundamental parameters λ_1, λ_2, and K. (Recall that $\rho = \exp(-K)$).
(2) Calculate the $\mu_{j\alpha}$ from (3.3) using L_1, L_{N_J}, and ρ.
(3) Calculate the $q_{ij\alpha}$ from (3.2) using $\mu_{j\alpha}$ and $\sigma_{j\alpha}$.
(4) Calculate the $Q_{i\alpha}$ from (3.5) using $q_{ij\alpha}$ and $p_{j\alpha}$.

Additional Model Structure

For some length frequency data sets, the sampling procedure or the fishery does not select the smallest fish in the first age-class. The effect of this size selectivity is that the mean length of the fish in the first age-class in the length frequency data set is larger than the mean length of the fish in the population. If this sampling bias is not accounted for, biased parameter estimates may be produced. We assume that size selective bias only occurs for fish in the first age-class and that it decreases linearly with age until the fish reach the second age-class.

$$(3.6)\quad \mu_{1\alpha} = L_1 + (L_{N_J} - L_1)\left(\frac{1-\rho^{1+(m(\alpha)-1)/12}}{1-\rho^{N_J}}\right) + b_1(12 - m(\alpha))/12$$

Estimating the Covariance Matrix of the Parameter Estimates

After choosing the model that best describes the data it remains to estimate how well the resulting parameter estimates are determined by the data. One method for doing this is to calculate an estimate for the covariance matrix of the parameter estimates.

Let $\hat{\boldsymbol{\Theta}}$ denote the maximum likelihood estimates for the parameters $\boldsymbol{\Theta}$. As an approximation to the covariance matrix for the parameter estimates $\hat{\boldsymbol{\Theta}}$ we have employed the inverse of the matrix of second derivatives of the log-likelihood function

$$(4.1)\quad \left[\frac{\partial^2}{\partial\theta_k \partial\theta_l}\left\{-1/2\sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_I}\ln(2\pi(\xi_{i\alpha}(\hat{\Theta})+.1/N_I)) + \sum_{\alpha=1}^{N_A}\sum_{i=1}^{N_I}\ln\left(\exp\left\{\frac{-(\tilde{Q}_{i\alpha}-Q_{i\alpha}(\hat{\Theta}))^2}{2(\xi_{i\alpha}(\hat{\Theta})+.1/N_I)\tau_\alpha^2(\hat{\Theta})}\right\}+.01\right) - \sum_{\alpha=1}^{N_A} N_I \ln(\tau_\alpha(\hat{\Theta}))\right\}\right]^{-1}$$

It should always be kept in mind that these variance estimates are in general only accurate to an order of magnitude. They do, however, allow the user to verify that the minimization procedure has indeed found a local minimum of the log-likelihood function. This is an important point. In a large model with many parameters it can be difficult to determine whether the putative minimum value of the parameters is indeed a minimum or whether the model has simply located a flat area of the log-likelihood function. If the matrix of second derivatives is positive definite, the point determined by the values of the parameters is located at a minimum rather than simply at a flat area.

User Interaction and the Avoidance of Incorrect Minima

One problem with nonlinear parameter estimation which does not occur with linear parameter estimation is the possibility of the existence of multiple minima of the objective function. The MULTIFAN procedure includes features which help to avoid the error of mistaking a local minimum for a true solution. These features are implemented through the use of extensive interactive graphics routines.

To illustrate the methods, consider the length frequency histograms for data set 1 in Fig. 2. The horizontal bars over the first two modes for length frequency subset No. 1 indicate the existence of user supplied bounds on the mean lengths for the first two age-classes. (Note that there are also bounds for the first two modes in subset No. 4, but they are obscured by the histogram itself). These bounds can be set by the user by viewing an interactive screen graphics representation of the histogram associated with each subset.

Now consider subset No. 3. The first mode for this subset is located at a somewhat larger length than normal for age-class 1 fish in month 4. This type of irregularity is normal for fisheries length–frequency data. Unfortunately, such irregularities in the mean length make it very difficult to create a completely automated process for fitting length frequency data. The reason for this is that the estimation procedure often can produce a better fit to the data by introducing an extra age-class into the part of the fit associated with the well defined modes which correspond to the first few age-classes. For this data set the model might be able to fit the data better by using three age-classes to fit the first two modes. This would enable it to obtain a better fit to the "irregular" data in subset No. 3.

To obtain "correct" fits to the tuna data it is necessary for the user to examine the pattern of modes in the length frequency data and to make some subjective decisions about the age-classes represented by them. For some data, if not most data,

this appears to be an unavoidable subjective component of the estimation procedure.

While the need to incorporate some subjective decisions into the length frequency analysis is unfortunate, MULTIFAN does provide a formal structure for expressing this subjective element in that any person can inspect Fig. 2 and make his or her own judgment about the appropriateness of the constraints used.

The accuracy of the parameter estimates which can be obtained by MULTIFAN depend in a complex fashion on many different characteristics of the data including between sample contrast in the proportions at age and modal separation. It is difficult to make any general statements about MULTIFAN's performance, but other factors being equal, the accuracy of the parameter estimates is very sensitive to the regularity of growth of the species being examined. If the mean lengths at age lie exactly on a von Bertalanffy curve, we have determined from an analysis of simulated data that it is often possible to obtain good parameter estimates without imposing constraints on the mean lengths. However, we have never encountered any actual fisheries data which exhibits this kind of regularity. For this reason, we feel that while it is useful to analyze simulated data in the initial developemnt stages of a model such as MULTIFAN (or indeed in the development of any statistical model), the suitability of MULTIFAN for real fisheries data is better determined by applying it to actual data where alternate estimates of the parameters are available.

The user should generally set quite wide bounds on the mean lengths. Fish growth is always somewhat irregular, and the mean lengths at age will not in general lie exactly on a von Bertalanffy growth curve. If the bounds are made too tight, the model may not be able to find any growth curve which satisfies the constraints. This will put the estimation scheme under considerable tension and distort the results obtained. Also, one irregular mode may exercise undue influence on the fit to the data. The bounds are set sufficiently tight to insure that the correct age-class is associated with a mode but not so tight as to require that the mean length at age lies exactly over a mode.

If the initial search for possible fits to the data does not cover a large enough region of parameter space, a local minimum of the objective function may be mistakenly accepted as the global minimum. To reduce the probability of incorrectly accepting a local minimum, the parameter space is partitioned into partially overlapping subregions and the log-likelihood function is minimized within each subregion. The variables used to set up such a systematic search are the number of age-classes assumed to be present in the data sets and different user selected initial values for the von Bertalanffy K. This procedure also provides an objective method for determining the number of age-classes presumed to be present in the data sets. A more detailed discussion of the systematic search estimates is presented in the description of the application to southern bluefin tuna below.

Hypothesis Testing

The problem of determining how many age-classes are represented in the data illustrates the combined use of systematic searches and hypothesis tests in the MULTIFAN model. For each initial estimate of K, models with increasing numbers of age-classes are fit. The increase in the maximum value of the log-likelihood function obtained by adding each age-class is calculated. If the increase is large enough the extra age-class is included in the model. This process is repeated until adding an extra age-class doesn't lead to a significant increase in the maximum value of the log-likelihood function.

A χ^2 test is used to determine what constitutes a significant increase in the maximum value of the log-likelihood function. We have employed the standard theory which states that under the hypothesis that the present model is the correct one (and the additional age-class is superfluous), if r parameters are added to the model, then twice the increase in the maximum value of the log-likelihood function is asymptotically distributed as a χ^2 random variable with r degrees of freedom.

Two types of errors can be made when making a decision based on a significance test. We could accept an extra age-class into the model description when the present number of age-classes is correct (type 1 error) or we could reject the extra age-class when it is actually present in the mixture (type 2 error).

Rosenberg and Beddington (1987) have investigated the performance of Sparre's model using simulated data. They reported that better estimates of the von Bertalanffy K parameter were obained when the number of age-classes in the mixture was overestimated rather than underestimated. Therefore, when determining the number of age-classes, a type 2 error is more serious than a type 1 error. To reduce the probability of occurrence of a type 2 error, we have employed the 0.90 point of the χ^2 random variable rather than the more conventional 0.95 point.

We do not recommend using the 0.90 point for testing the significance of the inclusion of other parameters such as the parameter for length-dependent standard deviations into the model. We have used the 0.95 level for all other parameters.

Application to Southern Bluefin Tuna

Background Information

Southern bluefin tuna is a highly migratory species. They spawn in the waters between northwestern Australia and Java from September to March (see Fig. 1 and Shingu 1978). Immature fish (younger than 8 yr old) are mainly found off the coasts of Western and South Australia, Victoria, New South Wales, and South Africa. When the fish migrate from west to east, they are caught by Australian fishermen (Majkowski et al. 1981). In the process of this migration, some of the fish also emigrate from the nearshore waters off Australia to join the oceanic communities throughout the southern hemisphere (see Shingu 1978; Murphy and Majkowski 1981). These fish are subject to the Japanese and New Zealand fisheries.

Fishing and research into southern bluefin tuna in Australia go back to 1938. In the 1960s, commercial poling and, to some extent, trolling of juveniles off New South Wales, Victoria, and South Australia (see Fig. 1) rapidly expanded into a major Australian fishery. With the expansion of the fishery off Western Australia and the introduction of purse seiners in the 1970s, the Australian annual catch increased from 10 000 to the maximum of 21 500 t in 1982. From that year, the catch has been declining due, at least partly, to catch restrictions. The catch in the 1988/89 season was limited to 5250 t.

The Japanese started to fish for southern bluefin tuna in the spawning ground in 1952 (see Fig. 1). In 1961, the Japanese catch peaked at 77 500 t with longlining extended to waters off the western, southern, and eastern coasts of Australia (see Shingu 1978). Since that year, the annual catch has declined to about 13 000 in 1987, in spite of very considerable further expansion of fishing grounds and effort.

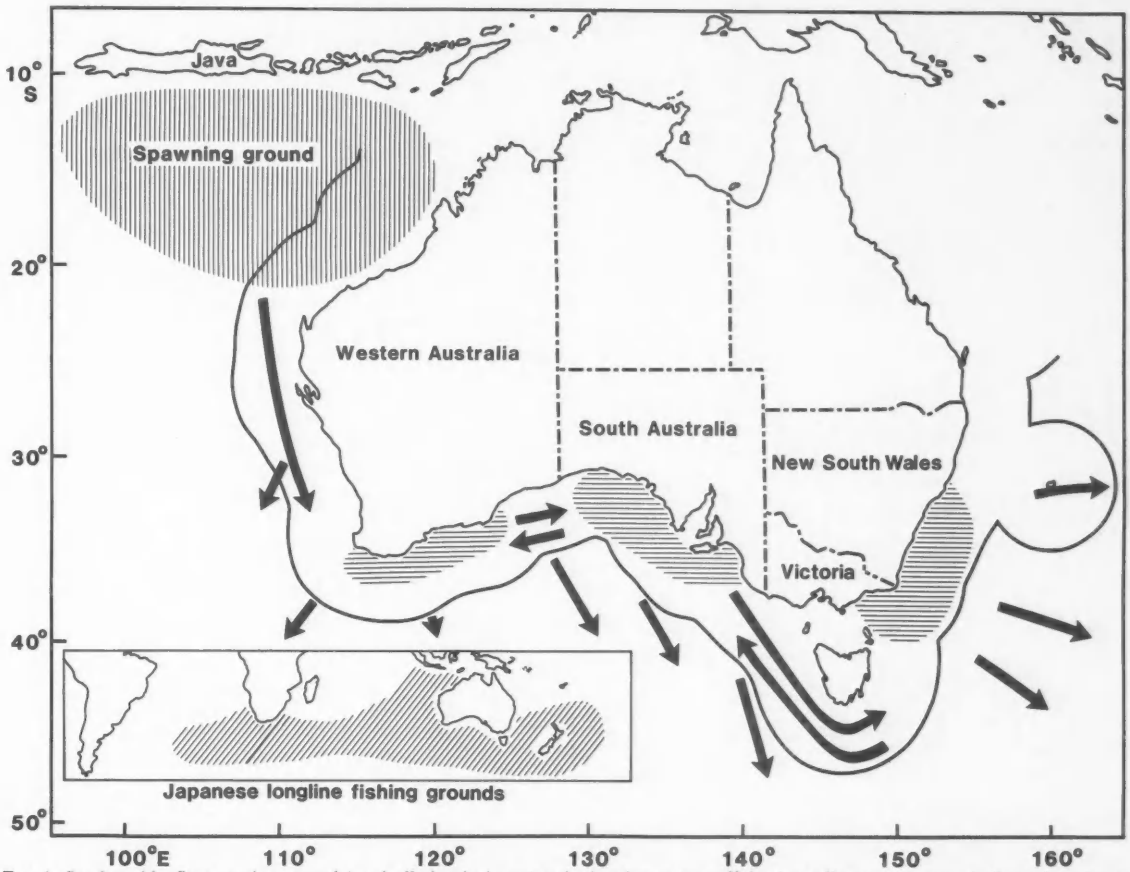

FIG. 1. Southern bluefin spawning ground (vertically hatched area) and migration pattern off the Australian coast (arrows indicate the primary direction of migration; the boundary of the 200-nautical-mile Australian Fishing Zone is indicated by the solid line) and the areas of operation of the pre-1982 Australian fisheries (horizontally hatched areas) and the Japanese fishery (diagonally hatched area).

The New Zealand southern bluefin tuna trolling and handlining fishery started in 1980 (see Gibson 1984). Its catches have been very small, below 200 t per year.

Because of the high economic value of southern bluefin tuna (prices of sashimi-quality fish reach over $100 per kilogram paid to Japanese fishermen), the population of this species has been significantly over-exploited (see Majkowski and Caton 1984; Majkowski 1985; Hampton and Majkowski 1986a; Caton and Majkowski 1987). It has been possible to identify this state of the population due to intensive research, including length sampling of catches (Majkowski 1985; Majkowski and Morris 1986) and tagging (see Majkowski and Murphy 1983c; Eckert and Majkowski 1987) carried out by Australian, Japanese, and New Zealand scientists.

Information on recaptures of tagged fish has allowed determination of an length–age relationship (see Kirkwood 1983; Hampton 1989). This relationship has been used to calculate ages from lengths for estimating global catch at age (see Majkowski and and Hampton 1983a, b). This estimation has been carried out for stock assessment purposes (see Majkowski and Hampton 1983c; Hampton and Majkowski 1986b).

The length frequencies of global catches have been derived on the basis of length samples weighted according to the magnitudes of gross catches in the different statistical areas and periods. Over the period of fishing, the systems for collecting and processing information on fish lengths and gross catches have been changing to adjust them to altering operations of individual fisheries (see Majkowski and Morris 1986). In the case of the Australian fishery, detailed length samples from the catches have been obtained while the fish were being unloaded or processed, depending on catch locations and periods. Sampling of Japanese catches has been carried out at sea and/or in ports when the catches are unloaded. In the case of New Zealand, all the fish caught have been measured at sea.

Two length frequency data sets, each containing 10 length frequency subsets, were made up from the length frequency data. Each subset consists of a weighted sum of many individual length frequency samples. The weights used were adjusted to represent the number of fish in the catch from the fishery from which each sample was taken. One data set was from the early years of the fishery (1963–66) while the other was from later years (1979–81). This partition was selected to investigate the consistency of the model estimates and to determine whether the model could detect changes in the exploitation pattern of

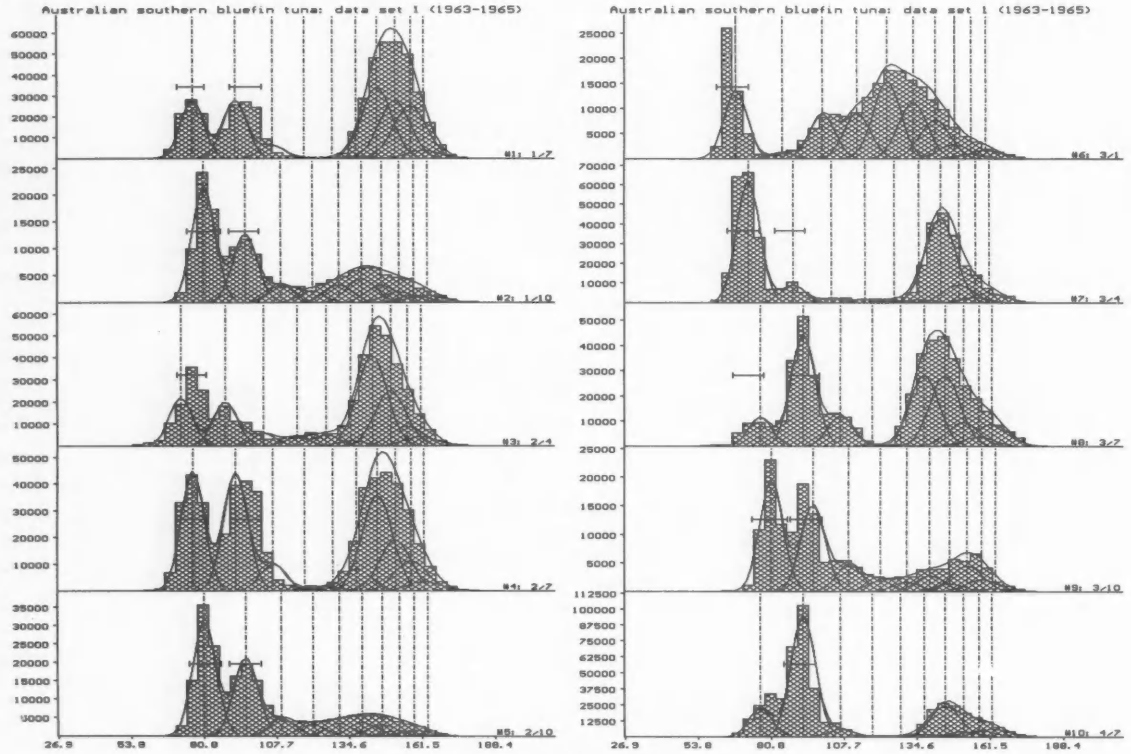

FIG. 2. Southern bluefin tuna data set 1.

the fisheries which may have occurred over time. The length frequency data are given in Appendix 1. The length frequency histograms for the two data sets are shown in Figs. 2 and 3. These data sets were analyzed separately and also combined into a single data set.

Setting up the Initial Systematic Search

The following discussion contains many references to the parameter estimates which are obtained by fitting the model with many different hypotheses to the data. For convenience we shall refer to the parameter estimates and associated log-likelihood function value obtained when fitting the model associated with a particular hypothesis to the data as a "fit."

Some of the most important user inputs to the MULTIFAN model occur at the initial stages of the analysis. Decisions, based on biological considerations, are made which affect the whole subsequent estimation process. These are the kinds of model inputs which are very difficult to include into the computer program itself.

The length frequency data are collected into quarterly groupings. Since the MULTIFAN model measures time by month, each quarterly grouping must be associated with a month. The four quarterly groupings were associated with months 1, 4, 7, and 10. Month "1" is assigned to the quarter in which the youngest age-class enters into the fishery, that is the third quarter (July–September, the austral winter).

To appreciate the necessity for numbering the months properly consider what would happen if month 1 were assigned to the first quarter. In this case, the youngest fish would not appear in the data sets until month 7. For all data sets taken from months 1–6 the first age-class would not occur. Unless the model is "told" that the first age-classes are absent in these data set, it may mistakenly attempt to fit the first mode with the first age-class. This problem can be avoided by requiring that the first age-class be empty for months 1–6, but this solution is rather artificial, involving the introduction of unnecessary extra constraints.

Another important user input involves setting constraints on some of the mean lengths to ensure that the model fits the obvious modes properly. We have placed bounds on the mean lengths for 17 of the first and second age-classes in the first data set and for 20 of the first, second, and third age-classes in the second data set. The bounds appear as horizontal lines over the modes in Figs. 2 and 3.

Even when the mean lengths at age are (correctly) constrained, the model can still fit the data incorrectly. It does this by estimating the proportion-at-age corresponding to a constrained mean to be very small and fitting that portion of the data with another age-class. To avoid this problem, lower bounds of 0.05–0.1 were placed on the proportions-at-age for the constrained age-classes. In general, it is not necessary to apply so many constraints, but doing so ensures that the model exhibits stable behavior between models with different hypotheses.

Numbers of age-classes and initial values of K are required to complete the specifications for the initial systematic search. By considering the distance between the first two modes in several of the length frequency data sets, it is clear that there are

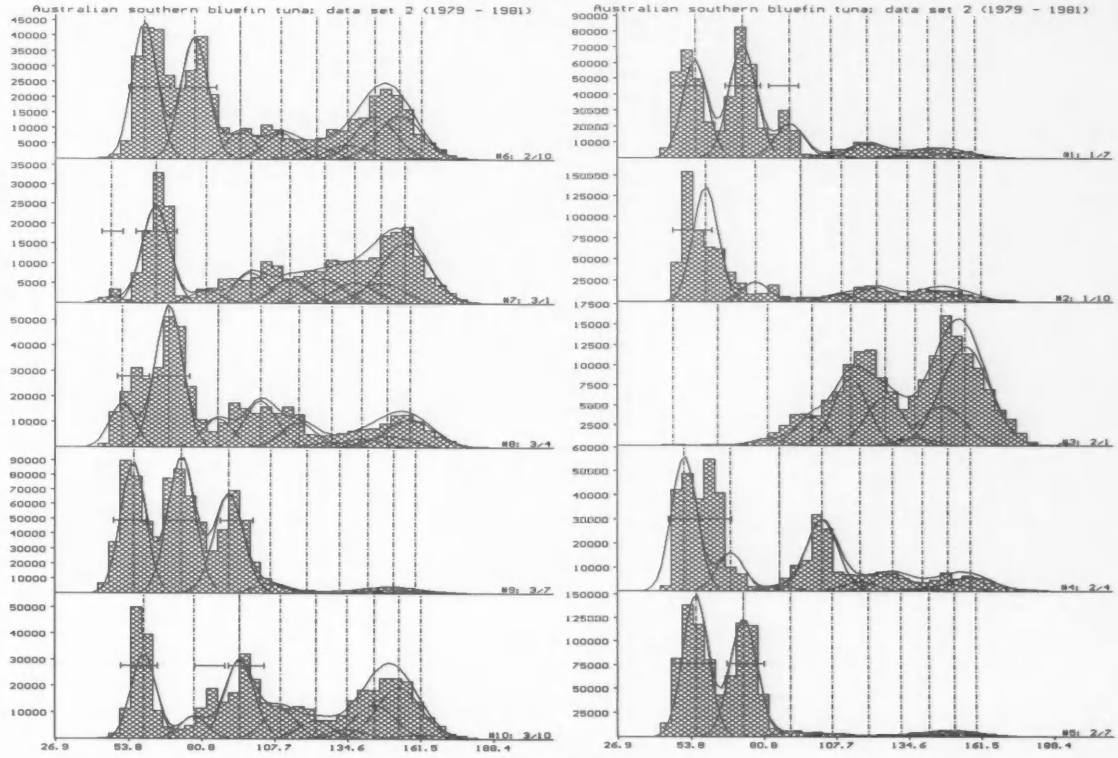

FIG. 3. Southern bluefin tuna data set 2.

at least six age-classes in the data. To illustrate the method we have fitted the data for all numbers of age-classes between eight and 13 inclusively. A species with at least six age-classes usually has an associated von Bertalanffy growth curve with a low value of K ($K < 0.25$ yr^{-1}). The values of K which were used in the systematic search were 0.06, 0.09, 0.12, 0.15, and 0.18yr^{-1}. Initially, the value of K was held constant at its initial value and the other model parameters were estimated. The result is a two dimensional array of fits, where each fit is determined by the number of age-classes and the initial value of K. For each number of age-classes (rows in Table 2), the parameters estimates from the best fit (the fit with the highest log-likelihood value) are used as the initial parameter values for estimating K.

TABLE 1. Summary of parameters estimated in each model. A + or − indicates whether or not the corresponding parameter is estimated in the model.

	Model			
Parameter	1	2	3	4
$p_{j\alpha}$	+	+	+	+
L_1	+	+	+	+
L_{N_J}	+	+	+	+
λ_1	+	+	+	+
λ_2	−	+	−	+
b_1	−	−	+	+
K	+	+	+	+

Results and Discussion

Fits for four different models which successively test combinations of two hypotheses concerned with the trend (λ_2) in standard deviation of the length at age around the mean length at age ($\sigma_{j\alpha}$) and first age-class size selectivity (b_1) were investigated. The composition of these models is summarized in Table 1.

Table 2 presents the complete systematic search results for Model 1 applied to data set 2. Entries in the body of the table are twice the value of the log-likelihood function (equation 2.3) and the number of estimated parameters. The parameters estimated in this table are the proportions at age ($p_{j\alpha}$, L_1, L_{N_J}, λ_1, and ultimately K. The first column is the number of significant age-classes included in the model. The next five columns show the log-likelihood function values obtained and the number of estimated parameters when K is fixed at the values shown. The best fit for each number of age-classes is underlined and the results of this fit are used as starting values for the estimation of K. There are 10 length frequency samples in each data set and the addition of one age-class to the model requires the estimation of one additional proportion at age for each sample in the data set. Therefore the number of parameters in the model increases by 10 for each age-class added. The last column of Table 2 shows the log-likelihood function values obtained and the number of estimated parameters when K is actually estimated. The values in this column are those used in hypothesis testing and are repeated in Table 4.

TABLE 2. Systematic search results for Model I ($\lambda_2 = 1$, $b_1 = 0$) applied to data set 2. Two times the log-likelihood values are shown for each model with the number of estimated parameters shown below in parentheses. The maximum value for each number of age-classes is underlined.

Number of age-classes	Values of K					Maximum over k
	0.060	0.090	0.120	0.150	0.180	
8	6435.23	6388.64	6274.63	6166.44	5919.80	6444.32
	(73)	(73)	(73)	(73)	(73)	(74)
9	7132.86	7118.85	7050.22	6919.66	6739.47	7137.60
	(83)	(83)	(83)	(83)	(83)	(84)
10	7127.25	7167.37	7134.90	7037.74	6871.53	7168.20
	(93)	(93)	(93)	(93)	(93)	(94)
11	7110.98	7165.54	7180.72	7107.87	6964.24	7184.04
	(103)	(103)	(103)	(103)	(103)	(104)
12	7093.48	7151.60	7185.79	7152.50	7028.20	7186.96
	(113)	(113)	(113)	(113)	(113)	(114)
13	7080.46	7134.25	7177.57	7174.39	7070.14	7185.39
	(123)	(123)	(123)	(123)	(123)	(124)

TABLE 3. Summary of hypothesis testing for fits for four models to data set 1. Log-likelihood function values with a single underline are the best fits for each model. The overall best fit is in boldface.

Number of age-classes	Model tested			
	Model 1	Model 2	Model 3	Model 4
8	6944.92	6985.42	6944.89	6984.99
	(74)	(75)	(75)	(76)
9	6970.95	7049.31	6970.92	7049.28
	(84)	(85)	(85)	(86)
10	7033.90	**7076.20**	7033.87	7076.17
	94)	(95)	(95)	(96)
11	7066.84	7083.93	7066.82	7083.76
	(104)	(105)	(105)	(106)
12	7078.84	7087.71	7078.59	7087.67
	(114)	(115)	(115)	(116)
13	7084.77	7093.40	7084.75	7093.40
	(124)	(125)	(125)	(126)

TABLE 4. Summary of hypothesis testing for fits for four models to data set 2. Log-likelihood function values with a single underline are the best fits for each model. The overall best fit is in boldface.

Number of age-classes	Model tested			
	Model 1	Model 2	Model 3	Model 4
8	6444.32	6540.53	6466.34	6555.99
	(74)	(75)	(75)	(76)
9	7137.60	7173.55	7145.07	**7195.43**
	(84)	(85)	(85)	(86)
10	7168.20	7184.62	7178.65	7205.75
	(94)	(95)	(95)	(96)
11	7184.04	7190.41	7201.09	7216.63
	(104)	(105)	(105)	(106)
12	7186.96	7189.80	7211.47	7224.09
	(114)	(115)	(115)	(116)
13	7185.39	7187.19	7216.95	7226.98
	(124)	(125)	(125)	(126)

After the various forms of the model have been fit to the data, it is necessary to compare the results of several systematic searches and to decide which of the fits is the best one. In general, this problem is very difficult and lacks a completely objective solution. (see for example chapter 6 of Draper and Smith 1981, for a discussion of this problem for linear statistical models.)

We define the best fit in the following way:

(1) It should not be possible to add any new parameters which produce a significant improvement in fit to the model.

(2) It should not be possible to remove any parameters from the model without producing a significant degradation in fit.

Of course it is necessary to define what is meant by significant. Suppose that two fits are compared and that one fit contains r extra parameters. Under the hypothesis that the simpler model is the correct one, twice the difference between the values of the log-likelihood functions will be asymptotically distributed as a χ^2 random variable with r degrees of freedom. We have used the 0.90 level for the significance level for the number of age-classes and the 0.95 level for other parameters.

Table 3 summarizes the hypothesis testing for four different models for data set 1, that is, the results of four different systematic searches are compared. Table 4 contains the corresponding results for data set 2. For each model Tables 3 and 4 only contain the "Maximum over K" column from the systematic search result table (see, for example, the first column of Table 4 and compare with the last column of Table 2) which gives the log-likelihood function values when all parameters including K are estimated.

Consider column 1 of Table 3. Moving from the 8 to the 9 age-class model adds 10 parameters (one parameter for each sample). The 0.90 level for a χ^2 random variable with 10 degrees of freedom is 15.98. The difference in the value of the fit between the 8 and 9 age-class models is 26.03, a significant improvement at the 0.90 level. (Twice the value of the log-likelihood function has been used in all the tables to facilitate doing the significance tests.) Continuing down the first column for Model 1 there are significant improvements in fit at the 0.90 level until the 12 age-class fit which produces an improvement of only 12.00. The only candidate for the best fit is the 11 age-class model. Repeating this process for Model 2 in column 2 we retain the 10 age-class fit. For Model 3 the candidate for the best fit is the 11 age-class fit. For Model 4 the candidate for the best fit is the 10 age-class fit.

Until now we have narrowed down the list of possible candidates for the best fit by considering the improvement in the fit due to adding age-classes. Now consider the effect of adding one parameter (b_1) for first length bias. The 0.95 level for a χ^2 random variable with 1 degree of freedom is 3.84. The Model 3 fits can be removed from the list of candidates because the

TABLE 5. Summary of hypothesis testing for fits for four models to the combined data set. Log-likelihood function values with a single underline are the best fits for each model. The overall best fit is in boldface.

Number of age-classes	Model tested			
	Model 1	Model 2	Model 3	Model 4
8	12888.33	12987.02	12903.91	13002.78
	(144)	(145)	(145)	(146)
9	13044.40	13061.74	13056.79	13080.37
	(164)	(165)	(165)	(166)
10	13095.46	13095.47	13117.30	13119.60
	(184)	(185)	(185)	(186)
11	<u>13123.92</u>	<u>13127.14</u>	13137.94	13141.48
	(204)	(205)	(205)	(206)
12	13151.34	13151.44	**13170.01**	<u>13171.05</u>
	(224)	(225)	(225)	(226)
13	13157.84	13163.81	13188.48	13188.61
	(244)	(245)	(245)	(246)
14	13157.66	13169.10	13196.15	13197.64
	(264)	(265)	(265)	(266)

Model 4 fits with the same number of age-classes produce a significant improvement in the fit. Now consider the 10 age-class fit for model 4. It can be compared to the 10 age-class fit for Model 2. The Model 4 fit has one more parameter than the Model 2 fit, but there is no improvement in fit. Therefore the 10 age-class fit for Model 4 is rejected. Finally the Model 1 candidate can be removed by comparing it to the Model 2 fit with the same number of age-classes. We are left with exactly 1 candidate for the best fit, the Model 2 fit with 10 age-classes.

This procedure leads us to accept a model which include length-dependent standard deviations and to reject the models which include the first length bias parameter. In other words the estimated value of λ_2 is significantly different from zero and b_1 is not significantly different from zero.

Table 4 summarizes the hypothesis testing for four different models for data set 2 by comparing the results of four different systematic searches. A similar process of comparing log-likelihood function values leads us to retain the 9 age-class fit to Model 4 as the best fit. This model includes length-dependent standard deviations and the first length bias parameter, b_1.

Table 5 summarizes the hypothesis testing for four different models for the combined data set. The process of comparing log-likelihood function values is similar to that previously illustrated except that adding one age-class in the combined data set increases the number of additional parameters by 20. The 0.90 level for a χ^2 random variable with 20 degrees of freedom is 28.41. The analysis proceeds as before except for Model 3. The difference between the 10 and 11 age-class fits is not significant, but the difference between the 10 and 12 age-class fits is 52.71 which is a significant improvement. (The 0.90 level for a χ^2 random variable with 40 degrees of freedom is 51.81.) Our rejection criteria leads us to retain the 12 age-class fit for Model 3.

The results of "best" fits to data sets 1 and 2 can be seen graphically in Figs. 2 and 3. In each figure, the sample number, year, and month are printed just above the right hand end of the abscissa. The observed length–frequency data are represented by the shaded histograms. The dashed vertical lines represent the estimated mean lengths at age in each sample. The inner smooth curves are the estimated numbers at age and the outer smooth curve is the estimated frequency distribution. The horizontal bars associated with certain modes are the bounds imposed on the mean length at age.

TABLE 6. Estimates from the best fits to data sets 1 and 2 and the combined data set.

	Data set		
	1	2	Combined
Log-likelihood function	7076.20	7195.43	13170.01
Estimated parameters	(95)	(86)	(225)
Significant age-class	10	9	12
L_∞	194.1	220.2	188.2
K	0.146	0.127	0.167
Estimated age	2.93	1.69	1.55
λ_1	5.06	6.43	5.20
λ_2	1.45	1.93	1.00
b_1	0.0	4.7	3.8

The parameter estimates produced by the "best" fits presented in Tables 2–4 for the three data sets are presented in Table 6. Previous estimates of L_∞ and K are presented for comparison in Table 7. The estimates produced by MULTIFAN are within the range of previously published estimates.

The effect of including a larger number of samples in the data set can be seen in Table 6. The parameter estimates based on the combined data set are not simply values which are intermediate to those obtained for the isolated samples. The estimate of L_∞ is smaller and that of K is larger than the corresponding estimates from either of the two smaller data sets. These parameter estimates correspond well with the more recent estimates from tagging studies (Hampton 1989). The MULTIFAN estimation procedure is able to resolve 12 significant age-classes using 20 samples compared with only nine or 10 significant age-classes using 10 samples. Tagging studies of southern bluefin tuna have shown that there are occasional individuals which are older than 15 yr (Anon. 1981).

The results for data set 2 and the combined data set indicate that the first length bias parameter is significantly different from zero. The results from data set 1 did not estimate a significant first length bias parameter. This result is not surprising because this data set does not include the length data from the Western Australia fishery which exploited smaller fish. The combined data set results also indicate that the standard deviation of the length at age around the mean length at age ($\sigma_{j\alpha}$) is constant over all age-classes.

Since the model is not given the age of the first age-class, it is impossible to estimate the usual t_0 parameter associated with the von Bertalanffy curve. Instead, if it is assumed that the von Bertalanffy curve passes through zero at age zero, i.e. $t_0 = 0$, then the age of the first age-class present in the data sets may be estimated. This parameter, designated by "estimated age" in Tables 6 and 8, is estimated to be 2.93 for data set 1 and 1.69 for data set 2. The fishery represented in data set 2 exploited fish about 1 yr younger than the fish exploited by the fishery represented by data set 1. Indeed data set 2 pertains to a period of time when there was an active fishery off Western Australia which exploited fish in a region through which younger fish are known to move.

Large bias in the estimates of K and L_∞ can occur if size selectivity is not accounted for. In this case, the only candidates for best fit are fits of models 1 and 2 which do not include the first length bias parameter (b_1). For data set 1, excluding size selective bias has no effect because the Model 2 fit is the best overall fit in any case (see Table 3). For data set 2 excluding

TABLE 7. Previous estimates of southern bluefin tuna growth rate parameters; adapted from Hampton (1989).

Reference	Method	Parameter L_∞	Parameter K
Shingu 1970	Length frequency	222.5	0.140
	Tagging	187.4	0.149
Yunkinawa, 1971	Scales	219.7	0.135
Hynd and Lucas 1974	Length frequency	220.0	0.150
Lucas 1974	Mark frequency	171.5	0.187
Murphy 1977	Tagging	180.8	0.146
Hearn 1979	Tagging	178.6	0.117
Kirkwood 1983	Tagging	209.0	0.125
	Length frequency	214.8	0.133
	Combined	207.6	0.128
Thorogood 1986	Otoliths	261.3	0.108
Present study	Combined	188.2	0.167
	Data set 1	194.1	0.146
	Data set 2	220.2	0.127

TABLE 8. Estimated standard deviations and correlation matrices for the parameter estimates.

Parameter	Standard deviations	Correlation coefficients L_∞	K	Estimated age
		Data set 1		
L_∞	1.69	1.00		
K	0.0030	−0.964	1.00	
Estimated age	0.0086	0.186	−0.438	1.00
		Data set 2		
L_∞	5.12	1.00		
K	0.0059	−0.957	1.00	
Estimated age	0.012	0.142	−0.423	1.00
		Combined data set		
L_∞	1.24	1.00		
K	0.0038	−0.863	1.00	
Estimated age	0.0046	−0.427	−0.080	1.00

size selectivity leads to the adoption of the Model 2 fit with nine age-classes as the best fit, rather than the Model 4 fit with nine age-classes (see Table 4). For the Model 2 fit, $K = 0.087$ and $L_\infty = 270.6$ which are substantially different from previous estimates. The estimate of K appears to be too low while that of L_∞ appears to be too high. This result is what one would expect if size selectivity is not accounted for.

The estimated standard deviations and correlation coefficients between the von Bertalanffy growth parameters are presented in Table 8. The estimated standard deviations for the parameter estimates appear to be unduly optimistic. They do indicate however that the likelihood function has a well defined minimum at the point determined by the parameter estimates.

Conclusions

The parameter estimates obtained by the MULTIFAN method agree well with estimates of the same parameters estimated from tag return data, scale analysis and otolith analysis. This illustrates sophisticated length-based analysis can provide the same information for managers as these more expensive and time-consuming conventional methods. Of course, when possible, it is always advisable to age at least a few fish to ensure that the results obtained by indirect methods such as length frequency analysis are reasonable. Indeed, it is possible to extend MULTIFAN to combine length-age data with length frequency data in a manner similar to that described in Fournier (1983).

The use of a robust likelihood based statistical model of length frequency data offers a number of important advantages. The MULTIFAN method integrates a powerful nonlinear parameter estimation technique with a formalized set of rules for evaluating alternative structural assumptions of the model. The result is an extremely powerful and sophisticated conceptual approach to the analysis of fisheries data.

The ability to simultaneously analyze a large set of samples to produce global parameter estimates increases the sensitivity of the analysis. The numbers of significant age-classes which can be resolved is increased. Parameters which may be ambiguously estimated by analyzing smaller data sets are also more satisfactorily resolved by analyzing a large number of samples.

For information about MULTIFAN contact Otter software, Box 265, Station A, Nanaimo, B.C. V9R 5K9, Canada.

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Appendix

Data set 1 Length frequencies

Number of data sets 10		Number of length intervals 90		Width of length intervals 2		Shortest length 30.50 2			
1963 year 1	quarter 1 month 7								
0	0	0	0	0	0	0	0	0	19
0	9	13	98	113	83	135	416	986	3640
8600	13195	15012	13547	12161	9674	6572	5190	5644	8511
12140	13813	13162	14036	14283	10339	6600	2961	1692	1000
690	605	592	370	479	239	143	245	220	524
1116	1508	4981	8065	14265	14891	19117	29341	24676	31264
27646	28453	27582	22590	19384	12625	9063	8426	4634	1928
1317	655	422	189	50	25	25	0	0	0
0	0	0	0	0	0	0	0	0	0
1963 year 1	quarter 2 month 10								
0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	35	68	89
561	1306	3427	6582	11504	12802	10492	6844	4752	3887
4444	5900	6151	5731	5047	4009	2669	2140	1866	1735
1457	1490	1546	1473	1143	1113	1652	1881	2034	2177
2308	2609	2861	3072	3107	3428	3546	2973	2693	2412
2333	2360	2403	2024	1380	1273	1086	1057	594	686
417	226	110	63	99	34	16	31	0	0
19	0	0	0	0	0	0	0	0	0
1963 year 2	quarter 4 month 4								
0	0	0	0	0	0	0	0	0	0
0	78	324	426	833	736	654	1983	5002	5574
8026	10996	16235	19846	14934	10439	5819	6806	9306	3964
5770	5763	5894	4891	4046	2712	1687	1517	1499	2067
2291	1952	2143	2150	2882	3427	2426	3519	2218	3344
4261	5309	8402	12502	19263	22180	26908	27924	26322	23869
20285	17176	15118	10520	8806	5824	4808	2653	1401	1249
596	306	409	230	82	69	55	41	14	0
0	0	0	0	0	0	0	0	0	0

1964 year 2 quarter 1 month 7

0	0	0	0	0	0	0	0	0	28
0	13	20	148	173	126	205	629	1496	5542
18124	20126	22894	20617	18488	14702	9976	7878	8572	12942
13482	21021	20002	21322	21644	15680	10053	4492	2563	1575
1106	1032	1011	565	1018	911	439	1202	916	2478
3798	3605	9538	9216	19700	18880	18278	24033	20719	23814
21957	18251	18513	11880	9052	8784	4873	4430	2020	1545
937	839	405	245	400	55	0	0	0	0
0	0	0	0	0	0	0	0	0	0

1964 year 2 quarter 2 month 10

0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	54	105	136
872	1996	5234	10072	17011	18715	15114	9409	6144	5858
6957	9523	10034	9462	8660	6551	4585	3834	2943	2306
2100	1957	2250	1929	2113	1845	1784	2305	2123	2543
2426	2781	2904	2692	3040	2668	2913	2926	2648	2683
2180	1917	1783	1651	1624	1200	878	681	449	290
195	100	64	15	21	6	0	6	0	0
0	0	0	0	0	0	0	0	0	0

1964 year 3 quarter 3 month 1

0	0	0	0	0	0	0	0	0	0
0	0	0	0	201	2348	11186	14888	3768	4764
3345	1667	639	316	347	309	311	678	620	1149
1426	2264	2836	3287	4233	4037	4258	4696	4000	4519
4348	4956	6401	5893	7138	8023	7925	9769	8497	9007
8339	7388	8067	6313	6276	5543	4973	4980	3347	3036
2518	2082	2254	1246	1124	903	740	668	512	354
176	252	32	20	11	10	10	31	10	21
0	0	0	0	0	0	0	0	0	0

1964 year 3 quarter 4 month 4

0	0	0	0	0	0	0	0	0	0
14	0	56	97	331	1095	3767	11509	26977	37274
35169	31370	21484	11820	4702	2233	2889	4378	6143	4647
3248	2270	1540	1217	1125	1183	971	1310	1207	1370
737	1068	888	739	1162	741	1014	899	1017	2001
2140	3392	8616	10851	17833	23026	21235	24469	19138	15465
12911	6250	8100	6424	5120	2509	2005	2107	1975	1577
547	391	281	37	67	92	0	38	0	19
0	0	0	0	0	0	0	0	0	0

1965 year 3 quarter 1 month 7

0	0	0	0	0	0	23	0	0	35
30	115	130	240	277	319	199	524	1538	3772
4527	4659	5161	4394	4006	3895	4094	6158	12506	21770
27688	24054	17728	10487	6982	5997	6394	6900	6180	5516
4729	2676	1653	727	387	305	384	564	2618	5508
8610	12461	16846	20210	21657	20580	21183	22692	19564	15627
13378	10954	10399	8844	8208	5943	5194	3456	3314	2628
2174	1297	488	215	214	50	118	0	0	0
0	0	0	0	0	0	0	0	0	0

1965 year 3 quarter 2 month 10

0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	21	58	63	62	32
288	854	3453	7450	12538	10549	6961	4945	4778	5704
8720	10201	8621	5099	2812	2434	2749	2839	2716	2831
2332	2052	1701	1338	1510	1077	1058	1177	1408	1270
1312	1297	1715	2164	2082	1893	1923	2097	2132	3585
2869	2610	4218	2488	2899	1401	844	919	677	396
217	223	119	76	82	1	21	5	15	21
0	0	21	0	0	0	0	0	0	0

1966	quarter 1
year	month
4	7

0	0	0	0	0	0	0	0	0	0
0	0	8	0	28	130	143	213	714	2272
5516	8484	11303	13302	16934	16776	14609	15534	26492	44101
57142	46095	25979	12273	6724	5239	5748	5583	4033	2128
1195	701	510	640	648	666	688	546	433	523
813	2055	3979	6364	9448	12558	13185	13375	12511	12239
10247	8697	8102	7337	6088	6032	4101	3911	2659	1986
1327	696	674	301	198	95	15	0	0	0
0	0	5	5	12	0	0	0	0	0

Data set 2 Length frequencies

Number of data sets	Number of length intervals	Width of length intervals	Shortest length
10	90	2	30.50

1979	quarter 1
year	month
1	7

0	0	0	0	0	65	338	6215	23036	31273
35725	32785	30543	19757	13158	9794	8903	8442	15025	23960
37175	46912	37781	21853	12364	6631	5760	9710	13741	16632
11689	5894	1608	976	1110	888	1767	2217	2703	2854
2606	3060	4796	5423	5452	3136	3383	3156	3485	2811
2183	1471	2055	3283	2760	2826	2691	3233	3757	2631
2113	1834	1834	2605	1412	1072	636	561	630	301
276	199	73	73	53	26	26	26	0	0
0	0	0	0	0	0	0	0	0	0

1979	quarter 2
year	month
1	10

0	0	0	0	0	0	315	406	8080	38282
81826	72901	49552	34125	35582	29178	36769	25839	15167	19974
13483	8436	4729	4177	4424	5150	10066	9683	4549	1747
1537	2064	2750	1890	2298	1987	2327	4368	3629	5567
4363	5222	8689	8741	10163	8870	6001	6681	5900	5136
3780	3400	4941	6747	7335	8313	6459	7758	6761	6348
7365	6149	3541	5366	3154	3205	2674	1457	1514	1086
1714	905	201	315	103	279	282	97	61	1
92	31	92	0	31	0	0	0	0	0

1979	quarter 3
year	month
2	1

0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	10	10	10	20
20	101	120	302	211	442	903	730	1196	1349
1637	2217	2022	1936	1938	1789	2414	3274	3332	3439
4548	5544	6081	5658	6463	5481	4662	3797	3494	3213
2187	2355	2043	4172	4083	4178	5268	5971	6517	9639
6462	7215	5282	6193	5320	4368	3210	3842	2120	2333
2605	734	1233	371	169	328	7	74	0	82
162	162	0	0	0	0	0	0	0	0

1979	quarter 4
year	month
2	4

```
    0     0     0     0     0     0     0  2082 12487 29702
31389 17484 20624 17741 21354 33730 31697  9186  5822  4381
 4707  2533  1157   814  1051   871   641   916  1715  3845
 5338  5460  5390  7680 14128 17914 15970 10002  4852  3253
 3313  3807  3218  3638  3716  3437  3759  4398  4206  4216
 3191  2403  2160  1871  1996  1669  1887  2735  3375  4456
 2296  2852  3305  3206  3148  2123  1521  2017   999  1151
  632   695   672   239   563   195   325    65     0    65
    0     0     0     0     0     0     0     0     0     0
1980 quarter 1
year month
   2     7
    0     0     0     0    63   195  4014 10405 30034 51982
68882 70393 62423 56064 47326 33285 22053 21899 26852 36876
48748 70781 63815 53646 32355 12330  5634  3016  3240  2194
 2863  3626  1795  2231  2346  2558  1329  1584  1581  2056
  936   824  1241   493  1020   513   640  1558   886  1431
  866  1009  2233  1875  1892  1380  2544  3186  2564  3467
 2558  2588  2949  2828  1999  1438  1658  1034   709   676
  394   296   126   186   231    78    51   106    24    24
    0     0     2     0     0     0     0     0     0     0
1980 quarter 2
year month
   2    10
    0     0     0     0     0     0    36   368   650   788
 2111  3695 11458 21940 21189 21480 22409 19568 14922 12130
11261 11743 13328 15488 20472 19468 11778  9229  5566  4635
 3639  4587  5663  4342  5118  2677  5947  5207  4165  5568
 3729  3178  3318  3115  3635  2739  2934  4126  4680  5157
 5011  4359  6982  6214  7221  6410 10225 10644 10548 12477
11530  9521  8323  8072  5142  3330  3618  2033  1745  1766
  890   622   291   308   148   102    34    33    11     0
    0     0    34     0     0     0     0     0     0     0
1980 quarter 3
year month
   3     1
    0     0     0     0     0     0  1249    91  2049  1378
  410   512  2234  5473  8748  9540 17701 15378 14268 10152
 1331   410   385   885  1431  1997  1597  2245  2616  3403
 2977  3339  2757  2964  4024  2591  5536  5076  4289  5176
 3426  2886  3260  3529  4019  4179  4433  3647  5559  5441
 5571  5140  5706  5095  5790  5040  6145  5433  7561  9664
 9557  8523  9513  9838  7024  5124  3888  2739  2222  2444
 1848   909   784   379   261   178    68     0    15     0
   25     0     0     0     0     0     0     0     0     0
1980 quarter 4
year month
   3     4
    0     0     0     0     0     0   404   983  6569  7376
11942  9952 13143 18263 14832 12121 11756 19851 21592 29792
27944 19501 15954  8071  6637  4333  3471  2744  3707  6070
 8398  9235  8799  6695  6537  6941  8046  8055  6948  6624
 7791  8472  7742  5337  2876  2270  2232  2505  2458  2484
 2679  3008  3666  3015  3877  3309  4133  3333  4397  4588
 6230  6575  6087  6956  4949  5361  4031  2680  2284  2116
 1657  1024   540   556   139   173   236   100    33   100
   33     1     0     0     0     0     0     0     0     0
1981 quarter 1
year month
   3     7
    0     0     0     0     0     0  1588  5254 10598 24005
39749 50222 42153 36942 27581 20654 16176 21957 31098 46746
44914 39333 33266 32355 26872 21181 17264 11504 18219 24869
34883 34429 29887 19565 12794  8248  6047  4414  3825  2255
 1863  1658  1298  1204  1177   940   781   685   742   919
  880   919  1060  1297  1495  1723  1658  1912  2031  2435
 2166  2050  2234  1659  1439  1233   907   985   849   786
  510   442   302   223   111    67    20    65    53   106
  106    53     5     0     0     0     0     0     0     0
```

1981	quarter 2								
year	month								
3	10								
0	0	0	0	0	0	61	326	830	1214
3404	7947	20021	30297	25901	13914	7247	3515	2221	2389
1578	2120	1911	3084	4583	6911	8314	10830	7975	5952
6951	10412	15633	16717	14687	8009	7393	6346	5750	6728
5934	5615	6359	5998	5902	5468	4135	3053	3079	4176
3781	5327	7024	7689	9025	9653	9031	9453	10443	12595
11821	11327	12125	9732	7502	6652	4034	4377	2865	2272
1031	909	714	483	348	137	148	47	0	0
0	0	65	0	0	0	0	0	0	0

Freshwater Migration as a Determinant Factor in the Somatic Cost of Reproduction of Two Anadromous Coregonines of James Bay[1]

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Lambert, Y., and J. J. Dodson. 1990. Freshwater migration as a determinant factor in the somatic cost of reproduction of two anadromous coregonines of James Bay. Can. J. Fish. Aquat. Sci. 47: 318–334.

We tested the hypothesis that the species-specific costs of migration differentially affect reproductive effort and somatic cost of reproduction in sympatric anadromous populations of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) of James Bay. Reproductive effort, which includes the energy cost of migration, is higher for cisco. Female cisco allocate more energy to reproduction than its total energy gain. The energy invested by lake whitefish in reproduction is approximately equal to its seasonal energy gain. Reproduction results in large differences in the energy content of gonads, viscera, and carcass between reproductive and nonreproductive fish of the same length. Neither cisco nor lake whitefish are able to spawn two years in succession. The somatic energy increase of reproductive female cisco is 121% lower than the somatic energy increase of nonreproductive females; similar comparisons are 89% (female) and 103% (male) for lake whitefish. The energy cost of migration is largely responsible for the higher somatic cost of reproduction observed for cisco. These different somatic costs of migration are related to resource accumulation prior to migration and to differences in the aerobic cost of swimming between the two species in combination with the difficulty of the freshwater migration.

Nous avons testé l'hypothèse selon laquelle, le coût énergétique de la migration avait une influence importante dans la détermination de l'effort reproducteur et du coût somatique de la reproduction chez les populations sympatriques anadromes du cisco (*Coregonus artedii*) et du grand corégone (*C. clupeaformis*) de la baie James (Québec). L'effort reproducteur, qui inclue le coût énergétique de la migration, est supérieur dans le cas du cisco. Les femelles du cisco allouent plus d'énergie à la reproduction qu'elles n'en accumulent au cours de la saison alors que chez le grand corégone, l'énergie investie dans la reproduction est approximativement égale à l'augmentation totale en énergie pendant la saison. De larges différences dans le contenu énergétique des gonades, des viscères et de la carcasse entre les poissons reproducteurs et non-reproducteurs de même taille sont observées. Le cisco et le grand corégone sont incapables de se reproduire pendant deux années consécutives. Les femelles reproductrices du cisco ont un investissement somatique en énergie inférieur de 121% à celui des femelles non-reproductrices; par comparaison, on observe des valeurs de 89% (femelle) et 103% (male) chez le grand corégone. Le coût énergétique de la migration est en grande partie responsable du coût somatique plus élevé de la reproduction chez le cisco. Cette différence dans le coût de la migration est reliée à l'accumulation d'énergie avant la migration et au différent coût aérobique de natation entre les deux espèces, associé à la difficulté de la migration en eau douce.

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The energy cost of anadromous migration is potentially an important parameter of fish reproductive patterns. This cost may influence fecundity, growth, and maintenance because energy devoted to migration will reduce energy available for other functions (Glebe and Leggett 1981). The theoretical basis of our study on sympatric anadromous populations of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) of James Bay (Québec) is that migration and reproduction are functionally related through partitioning of a limited energy resource. We hypothesized that the energy cost of freshwater migration, through its influence on reproductive effort and somatic cost of reproduction, is an important parameter in determining different reproductive patterns of anadromous coregonine populations.

Accessory activities, like spawning behavior, territoriality on the spawning grounds or live bearing of young, may be more important in reproductive effort than the production of gonads. In anadromous species, migration affects the somatic cost of reproduction and survival. This is demonstrated by the extensive energy depletion and high spawning and postspawning mortality in many anadromous fish species (reviewed by Glebe and Leggett 1981). Bell (1980) provides evidence of a correlation between the degree of anadromy (migration distance) and the rate of adult survival. The most anadromous species that make extensive ocean migrations are semelparous whereas the least anadromous species with oceanic migrations that are short and confined to coastal and estuarine waters are all iteroparous. However, the correlation between gonad/total weight ratio and the rate of adult survival was weak. Similar gonad/total weight ratios were found in both semelparous and iteroparous species

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suggesting the importance of the degree of anadromy in determining adult survival.

The anadromous populations of cisco and lake whitefish in James Bay provide an excellent opportunity to study the contribution of migration cost to reproductive effort and somatic cost of reproduction. In the Eastmain River (Fig. 1), cisco and lake whitefish migrate the same distance and use the same spawning grounds. The cost of migration, based on weight loss studies, is apparently high for both species largely due to the long period (2–3) mo) fish spend in the river without feeding prior to spawning (Dodson et al. 1985). In addition, the 7-km section of rapids fish must ascend to reach the spawning grounds may represent a major difficulty for both cisco and lake whitefish. A low metabolic scope for activity combined with a high net aerobic cost of swimming led Bernatchez and Dodson (1985) to conclude that the swimming performance of cisco and lake whitefish was poor compared with most salmonids. The higher net aerobic cost of swimming for cisco (Bernatchez and Dodson 1985) and its smaller size should result in a higher cost of migration compared with lake whitefish.

The purpose of this study was to test the hypothesis that the species-specific costs of migration differentially affect reproductive effort and the somatic cost of reproduction for cisco and lake whitefish. Because of their smaller size and greater swimming costs, we proposed that cisco's migration costs should be higher than those of lake whitefish resulting in a higher somatic cost of reproduction.

The specific objectives of this study were: a) to estimate the somatic cost of reproduction, first by estimating seasonal energy increase in reproductive and nonreproductive fish and second by estimating the reduction in somatic energy increase caused by reproductive effort; b) to estimate the importance of the energy cost of migration in the somatic cost of reproduction and; c) to calculate if the energy cost of migration was higher in cisco resulting in a higher somatic cost of reproduction compared with lake whitefish.

Materials and Methods

Sampling

Seasonal migration patterns of cisco and lake whitefish were documented between 1979 to 1981 by recording changes in catch per unit effort and length composition of gill net samples obtained from mid-May (spring thaw) to late October (winter freeze-up) in the Eastmain River and adjacent areas (Lambert and Dodson 1982a,b).

Seasonal changes in energy content associated with migration and reproduction were documented by quantifying absolute changes in weight and energy content for reproductive and nonreproductive fish sampled along their general migratory route. As neither cisco nor lake whitefish appear to spawn yearly once maturity is reached (Morin et al. 1982), reproductive and nonreproductive fish of similar lengths are common in the populations of both species. Sampling was conducted between May 1982 and May 1983 and concentrated on adult fish. Adult fish were defined as fish which exceeded the length at which 50% of the fish were mature (>26 cm for cisco and >34 cm for lake whitefish). Ten reproductive and 10 nonreproductive adults of each sex and each species were sampled whenever possible according to the following schedule: (a) spring break-up (15–30 May 1982) at the mouth of the Eastmain River (Fig. 1) during seaward migration of both species following overwintering; (b) mid-July to the end of July along the coast and in the vicinity of islands situated 15–20 km north of the river during the feeding migration of both species; (c) mid-August to the end of August at the mouth of the Eastman River for the return migration of spawning adults and along the coast north of the river for nonreproductive adults; (d) mid-September at the base of the first rapids (Fig. 1) for reproductive adults and along the coast for nonreproductive adults; (e) mid-October to the end of October on the spawning grounds for reproductive adults and below the rapids and at the river's mouth for nonreproductive adults entering into freshwater for overwintering; (f) early November below the rapids for spent fish; (g) spring break-up (May 1983) at the river's mouth to complete one annual cycle. Fish identified as reproductive individuals represent fish that were spawning in 1982.

Nonreproductive females were identified in the spring of 1982 by the presence of unresorbed eggs and flaccid appearance of the ovaries. These fish spawned in fall 1981 but were unable to spawn in 1982. The identification of nonreproductive males in the spring of 1982 was more subjective and was based on the flaccid appearance of the testes. Between July and November, maturity stages using the classification of Nikolskii (1963) and the gonadosomatic index (weight of the gonads as a proportion of body weight) were used to identify reproductive and nonreproductive fish. It is probable that fish identified as nonreproductive individuals between July and November include repeat spawners that had skipped spawning and late maturing virgin fish that never spawned as the two groups are indistinguishable during this period.

Sampling was done with experimental gill-nets measuring 45.7 m by 2.4 m and comprising six panels graded from 25 to 102 mm mesh size (stretched measure). After capture, fish were kept on ice and were processed within 5 h. For each fish, fork length was measured to the nearest 0.1 cm and otoliths removed for age determination. Gonad, viscera, liver, and carcass weight (whole eviscerated body, including head, skeleton and muscle) were recorded to the nearest 0.01 g and each tissue was individually frozen for further analysis of energy content in the laboratory. A total of 672 fish were processed and kept for energy content analysis.

Proximate Analysis

Energy content of each fish was determined by the energy equivalence of protein and fat content of gonad, liver, viscera and carcass. Determinations of protein, fat, and moisture content were made for each tissue that had been previously homogenized (whole tissue). Determinations were performed in duplicate (two homogenized tissue samples) and a mean value was calculated except for tissues weighing less than 1 g where only one determination each was made. The mean difference between duplicate samples as percent of wet weight was less than 1% for carcass fat, protein, and moisture content. For other tissues, the mean difference between duplicate samples for fat, protein, and moisture content was less than 2%.

Moisture content was determined by drying 1 to 25 g samples to a constant weight at 80°C. Fat content was determined by the method of Bligh and Dyer (1959) with samples of 25 g for carcass tissue. Gonad, viscera, and liver fat contents were determined for 2-g samples by the combination of two methods: extraction according to Bligh and Dyer (1959) and determination of fat content by the colorimetric method by Kibrick and Skupp (1953) as modified by Fales (1971). Total nitrogen con-

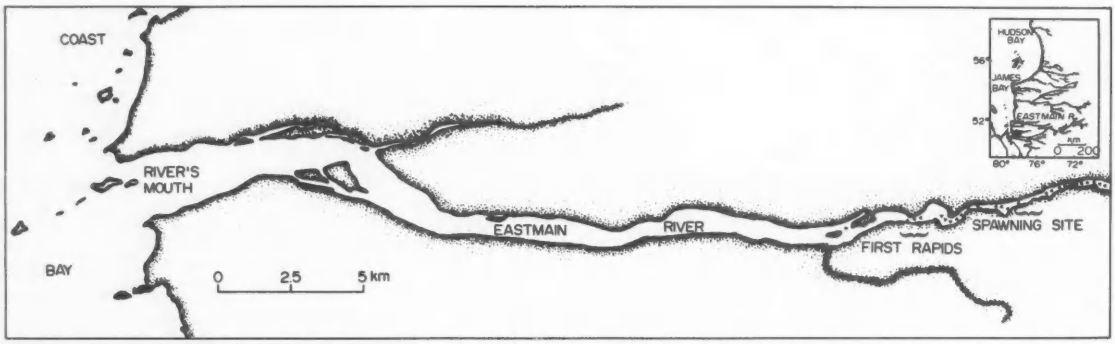

FIG. 1. Location map of the Eastmain River along the Eastern coast of James and Hudson bays with the indication of the spawning grounds for cisco and lake whitefish and position of the rapids.

tent was determined by micro-Kjeldahl digestion of 1-g samples followed by the Berthelot reaction (Haslemore and Rougham 1976; Dutil 1982). Correction for nonprotein nitrogen was done for the carcass (Niimi 1972). Protein content was estimated by multiplying nitrogen values by 6.25 (Dowgiallo 1975).

Energy contents were determined by applying the energy equivalents $2.4 \cdot 10^4$ J·g^{-1} for protein and $4.0 \cdot 10^4$ J·g^{-1} for fat (Kleiber 1975).

Energy Changes

Changes in energy content of different tissues at successive stages of migration were quantified by deriving linear regressions of tissue energy content on length (logarithmic transformed data) for reproductive and nonreproductive fish of each sex and species at each sampling site along the migratory route. Comparisons of the appropriate significant linear regressions were done by analysis of covariance (Sokal and Rohlf 1981). When the linear regression was not significant (slope not significantly different from 0), the mean value of tissue energy content and length were calculated. Comparisons between calculated mean values and predicted values of tissue energy content from linear regressions for the same length were done with *t*-test (Zar 1974).

Fat, protein, and energy of carcass and viscera utilized during freshwater migration and overwintering were estimated for both sexes and species. Calculations were made from observed values at the end of freshwater migration and overwintering and calculated values from linear regressions before freshwater migration and overwintering. Relative levels of fat, protein, and energy content between reproductive and nonreproductive individuals at the end of the season (October) were also calculated from observed values of reproductive individuals and calculated values from linear regressions for nonreproductive individuals. Interspecific comparisons were done with Mann–Whitney U-test (Sokal and Rohlf 1981).

Absolute energy changes for each tissue were determined from linear regressions at each sampling site for a standard fish of each species. The length of a standard reproductive or nonreproductive fish corresponds to the observed mean length of reproductive adults of each species at the time of spawning; 29.0 cm for cisco and 36.5 cm for lake whitefish. Otoliths were used to calculate seasonal increase in length and the length of standard fish at different periods of the season in order to take into account the growth of the "standard" fish. Methods for age determination and calculations of seasonal increase in length are described in Lambert and Dodson (1990).

Cost of Reproduction and Migration

Comparisons between somatic and reproductive investments of "standard" reproductive fish captured along the migratory route with those of "standard" nonreproductive fish were used to estimate reproductive effort, cost of reproduction, and cost of migration. These terms were estimated with the basic parameters defined by Tuomi et al. (1983):

l_n = the somatic energy increase of nonreproductive fish (which is equivalent to the total energy gain of nonreproductive fish)

l_s = the somatic energy increase of reproductive fish

l_r = the reproductive investment of reproductive fish

l_a = the total energy gain of reproductive fish ($l_s + l_r$).

Total energy gain represents the proportion of ingested energy (from feeding) available for growth and reproduction. The difference in total energy gain between reproductive and nonreproductive fish (R_a) was estimated by the difference between total energy gain of reproductive fish and somatic energy increase (total energy gain) of nonreproductive fish. Reproductive effort (R_e) was defined as the ratio of energy investment in reproduction on the maximum somatic energy content of reproductive fish. The absolute cost to somatic energy increase caused by reproduction (R_s) was estimated as the difference between somatic energy increase of reproductive and nonreproductive fish. The somatic cost of reproduction (RE_s) was measured by the extent to which reproduction reduced the somatic energy increase of reproductive fish below the level of nonreproductive fish.

The importance of the reproductive migration on somatic energy increase was estimated by evaluating migration effort and by comparing energy loss for migration and energy investment in the gonads. Migration effort (MG_e) was defined as the ratio of the energy loss for migration (MG) on the maximum somatic energy content of reproductive fish.

The basic parameters were estimated by energy changes of "standard" reproductive and nonreproductive fish. The somatic energy increase of nonreproductive fish (l_n) was calculated as the somatic energy increase (sum of carcass, viscera, and liver energy content) of nonreproductive fish between May and October 1982. The somatic energy increase of reproductive fish (l_s) was calculated as the net somatic energy increase of repro-

TABLE 1. Mean increase in length (mm) of reproductive (R) and nonreproductive (NR) cisco and lake whitefish of each sex of the same age. Cisco, 5 to 6 yr, lake whitefish, 6 to 7 yr.

		Mean (mm)	*SD*	*n*
Cisco				
Female	R	8.7	3.6	27
	NR	9.9	5.0	24
Male	R	10.9	5.7	36
	NR	11.2	3.3	10
Lake Whitefish				
Female	R	14.1	5.5	26
	NR	15.1	6.0	23
Male	R	15.8	7.0	33
	NR	18.0	6.3	9

ductive fish between May and early November 1982 (after spawning) following somatic energy depletion caused by reproduction. The reproductive investment of reproductive fish (I_r) was calculated as the sum of the energy increase in the gonads (I_g) between May and October 1982, the energy loss during spawning (due to spawning behavior and return of fish below the rapids after spawning) and the energy loss for migration (*MG*). The energy loss for migration was calculated as the difference between the somatic energy loss during freshwater migration (August to October for cisco and July to October for lake whitefish) and the energy increase in gonads during the same period of time (I_{gm}). The energy loss for migration between August and October was also calculated for lake whitefish (*Mg*) in order to compare the energy loss of both species during the period which fish ascend the rapids. Finally, the total energy gain of reproductive fish (I_a) was estimated as the sum of somatic energy increase and reproductive energy investment of reproductive fish.

The energy cost of overwintering (energy loss from November 1982 to May 1983; W_a for reproductive fish and W_n for nonreproductive fish) was also calculated as a proportion of the maximum energy content for both reproductive and nonreproductive fish. The total energy expenditures for migration, reproduction, and overwintering (TEC_r) were also expressed as a proportion of the maximum energy content.

Results

Increase in Length and Energy Changes

Within species, reproductive and nonreproductive individuals of both sexes of the most abundant age classes (cisco, 5 to 6 yr, lake whitefish 6 to 7 yr) showed similar increases ($P>0.05$) in length over the growing season (Table 1). Nonreproductive individuals did not appear to devote any of their surplus energy to increase their length. However, differences ($P<0.05$) in energy content between reproductive and nonreproductive individuals were observed during the growing season (Fig. 2). In May 1982, nonreproductive individuals of each sex (except for female lake whitefish) had lower energy content ($P<0.05$) than reproductive individuals measuring the same length. By the end of October nonreproductive fish had higher energy content ($P<0.05$) than reproductive fish due to the later's energy loss associated with freshwater migration and gonad maturation.

Cisco

In cisco, a significant increase ($P<0.05$) in total and somatic energy content was observed between May and August for reproductive fish prior to freshwater migration (Fig. 2). From August until November, when the fish spawn, there was a significant decline ($P<0.05$) in somatic energy content. During the same period, the energy content of the gonads increased to reach a maximum at the end of October (Fig. 3). Finally a decrease ($P<0.05$) in somatic energy content was observed during the winter (beginning of November to the end of May). In nonreproductive cisco, energy content increased ($P<0.05$) between May and October followed by a decline ($P<0.05$) during the winter.

In nonreproductive fish, no changes in gonad energy content ($P>0.05$) were observed during the season (Fig. 3). In reproductive females, maximum gonad energy content was reached near the end of October prior to spawning (387 kJ). Gonad development was not complete at river entry. An increase of 217 kJ (128%) in gonad energy content was observed between the end of August and the end of October during freshwater migration for females (Fig. 3). In males, the energy investment in the testes was much less (6 kJ) and the energy increase during freshwater migration was lower (32%).

Associated with maturation and freshwater migration, significant differences in carcass and viscera energy content were observed between reproductive and nonreproductive fish. In nonreproductive fish, increases in carcass and viscera energy content ($P<0.05$) occured during the summer and energy levels remained relatively stable until the end of October (Fig. 3). In reproductive fish, carcass and viscera energy ($P<0.05$) increased during the summer with the maximum level observed at the end of August. During the freshwater migration, carcass and viscera energy content declined ($P<0.05$). In female cisco (Fig. 3) carcass energy content decreased by 901 kJ (48%) and viscera energy content by 66 kJ (63%).

Carcass was the main source of energy used to complete gonad maturation and to fuel the freshwater migration. In female cisco, carcass energy decrease represented 92% of the total energy loss compared with 7% for viscera and only 1% for liver. In male cisco, the carcass energy decrease was 381 kJ (22%) but spent fish could not be sampled because the lower part of the Eastmain River froze before the end of spawning. As spawning activities can be costly, carcass energy decrease for male cisco was underestimated because the spawning period was missed. Even though underestimated, carcass energy was the main source of energy used during freshwater migration for male cisco and represented 83% of the total energy loss. The decline in viscera energy (67 kJ) for male cisco was similar to that of females following spawning suggesting that most of the energy available had been used prior to spawning. In fact, the energy level in male viscera did not change ($P>0.05$) from October 1982 to May 1983 (Fig. 3).

Comparisons between reproductive and nonreproductive cisco show that fish that did not reproduce reached ($P<0.05$) higher carcass and viscera energy levels in October even though they had significantly lower carcass and viscera energy in May (Fig. 3). After spawning (November), carcass and viscera energy reserves of reproductive females represented 58 and 17%, respectively of the carcass and viscera energy content of nonreproductive females. In males, carcass and viscera energy of reproductive individuals prior to spawning in October were also lower (72% of carcass energy and 23% of viscera energy) than those of nonreproductive males (Fig. 3).

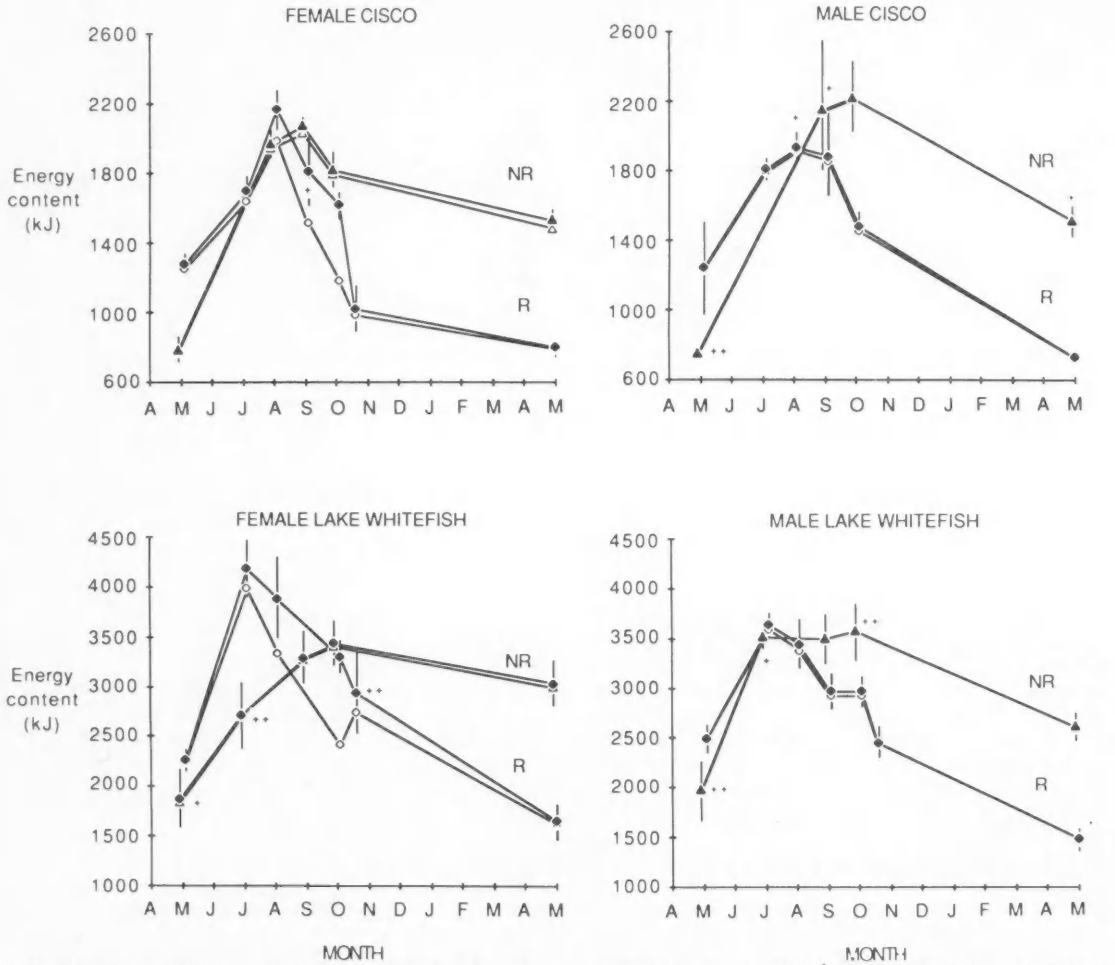

FIG. 2. Total and somatic content of standard reproductive (R) and nonreproductive (NR) cisco and lake whitefish sampled from May 1982 to May 1983 along their migratory route. Upper line (closed dots) indicates total energy content and lower line (open dots) indicates somatic energy content. Vertical bars indicate standard errors of total energy content derived from regression analysis. Regressions were significant at $P<0.05$ level except as indicated by + where $0.05<P<0.10$ and by + + where the regression was not significant; in such a case the mean value was presented. This convention is repeated in subsequent figures.

During overwintering, nonreproductive cisco rely on their carcass and viscera energy reserves but reproductive fish draw energy from their carcass energy reserves only (Fig. 3). In nonreproductive female and male cisco, 19 and 20%, respectively of the energy lost during winter came from the viscera energy reserves.

Lake whitefish

In lake whitefish, the same general pattern of total and somatic energy changes were observed (Fig. 2). The only difference with cisco was that the maximum energy level of reproductive fish was reached at the end of July instead of August. The analysis of variations in energy content of the different tissues (Fig. 4) indicate that female lake whitefish invested energy in gonads during freshwater migration. The increase in energy content of gonads between August and October was 347 kJ representing an increase of 66%. In males, the maximum energy content in the testes was observed before the freshwater migration (Fig. 4). The apparent energy decrease in testes during freshwater migration was not significant ($P>0.05$).

In nonreproductive males and females, significant increases in carcass and viscera energy content ($P<0.05$) occured between May and October 1982.

In reproductive males and females, carcass reserves were also the main source of energy to complete gonad maturation and freshwater migration. Carcass energy decrease of male and female lake whitefish represented 78% (895 kJ) and 75% (1172 kJ), respectively of the total energy lost during freshwater migration (Fig. 4). Viscera energy reserves used by male and female lake whitefish represent 19% (218 kJ) and 22% (345 kJ) of the total energy expended during freshwater migration. The liver was not an important organ for storage of energy, representing only 3% (48 kJ) of the energy used during freshwater migration.

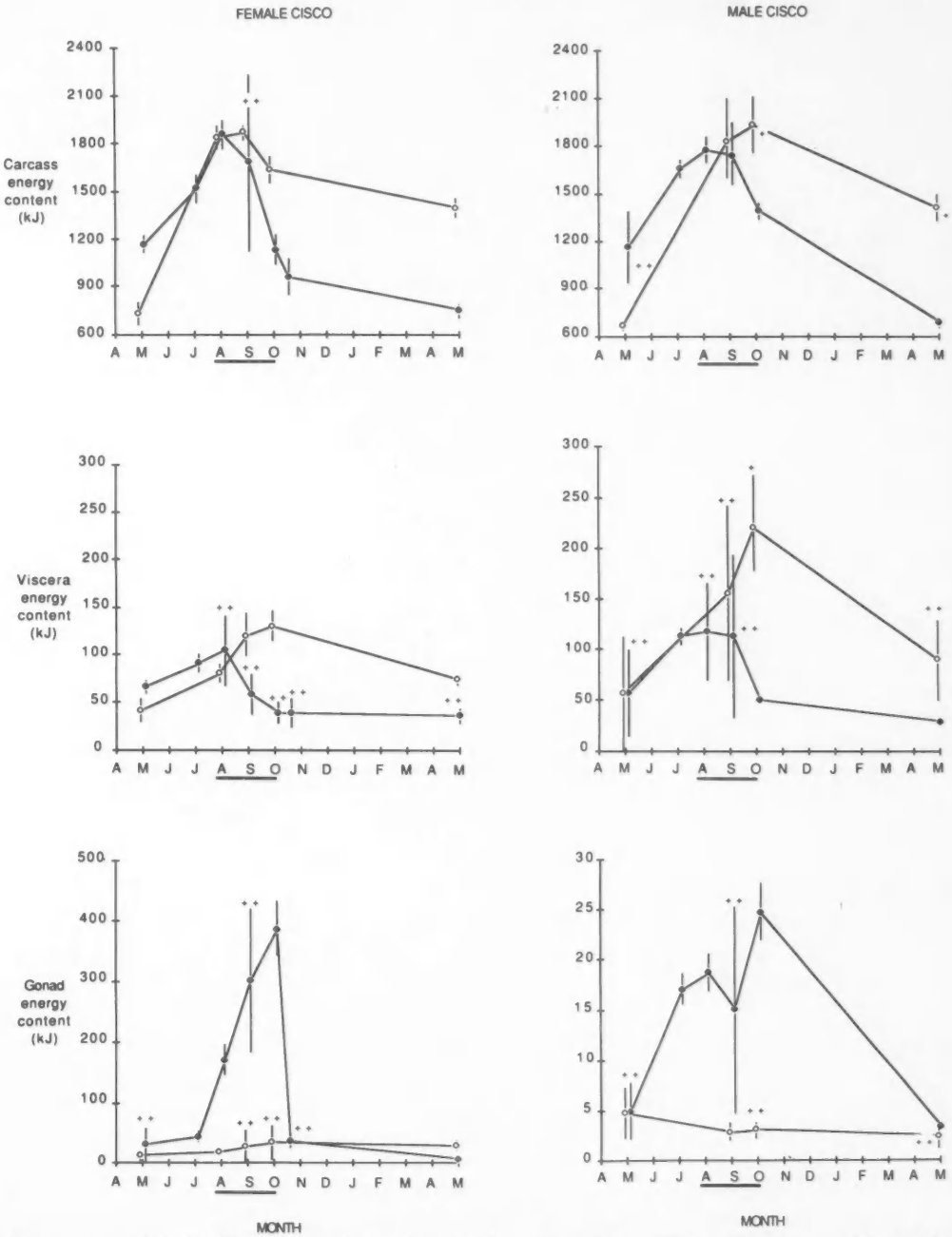

FIG. 3. Energy content (kJ) in the different tissues of standard reproductive (-◆-) and nonreproductive (-◇-) cisco sampled from May 1982 to May 1983 along their migratory route. Solid horizontal lines represent the period of time between the beginning of migration and the beginning of spawning.

While overwintering, nonreproductive lake whitefish used both their carcass and viscera energy reserves whereas reproductive individuals used only carcass energy reserves. Viscera energy reserves represent 16 (male) and 33% (female) of the total energy loss during the overwintering period for nonreproductive lake whitefish (Fig. 4).

Interspecific comparisons

Female lake whitefish used a smaller proportion of their carcass energy reserves and a greater proportion of their viscera

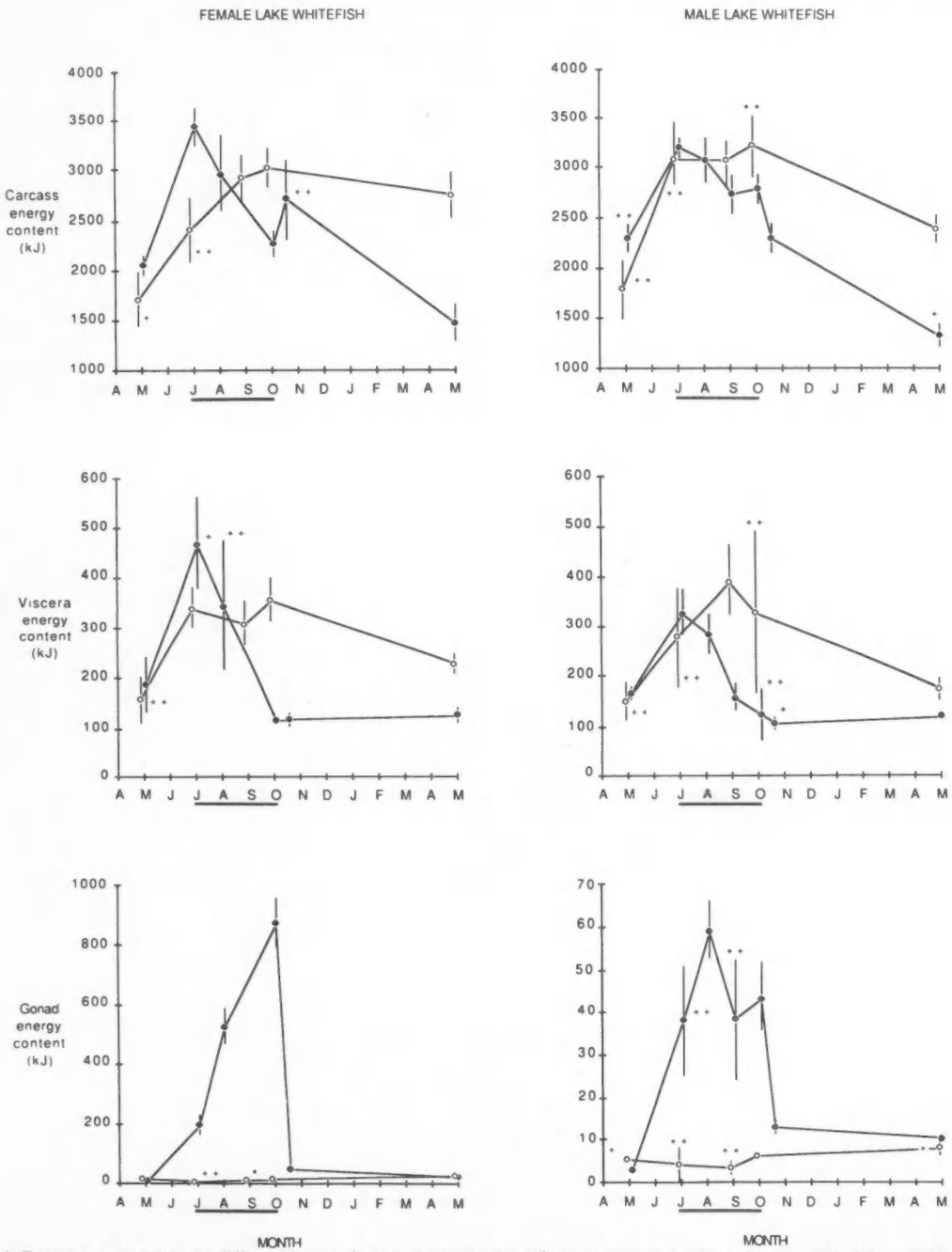
FEMALE LAKE WHITEFISH
MALE LAKE WHITEFISH
Carcass energy content (kJ)
Viscera energy content (kJ)
Gonad energy content (kJ)
A M J J A S O N D J F M A M
MONTH

FIG. 4. Energy content (kJ) in the different tissues of standard reproductive (-◆-) and nonreproductive (-◇-) lake whitefish sampled from May 1982 to May 1983 along their migratory route. Solid horizontal lines represent the period of time between the beginning of migration and the beginning of spawning.

energy reserves than did female cisco. Based on tissue energy content following freshwater migration and spawning (Fig. 5), female lake whitefish carcass and viscera energy decreased by 34 and 75%, respectively compared to 49 and 61% for female cisco. Comparisons between males after spawning could not be made because of the incomplete sampling of male cisco. However, comparisons of the data before spawning (Fig. 5) indicate that male lake whitefish used a greater proportion of their vis-

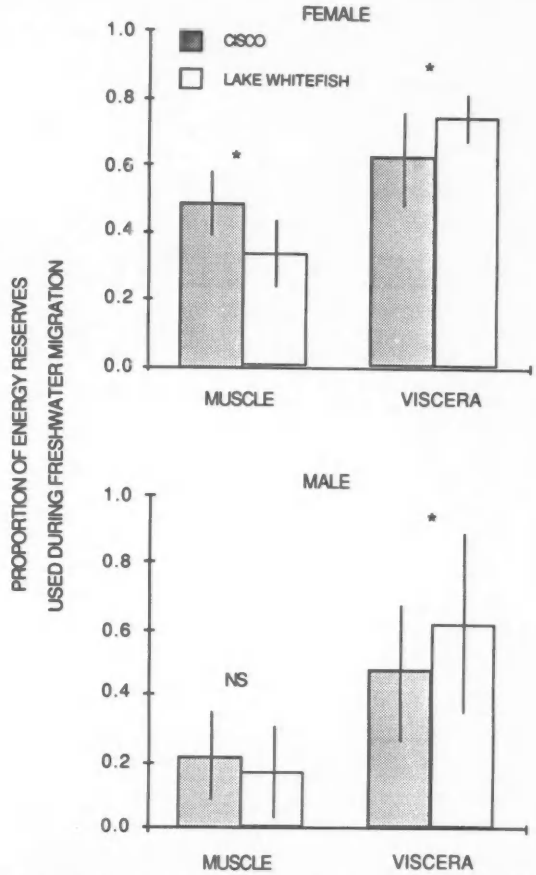

FIG. 5. Relative carcass and viscera energy decrease of reproductive cisco and lake whitefish during freshwater migration. Values are after spawning for females and before spawning for males. Significant differences between the two species are indicated by an asterisk (Mann–Whitney U-test; $P<0.05$).

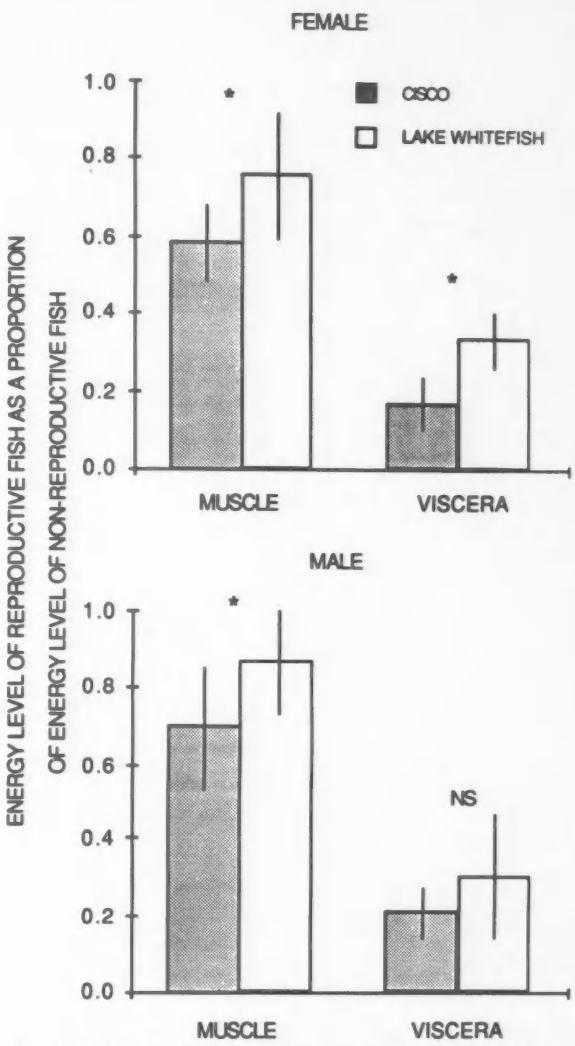

FIG. 6. Carcass and viscera energy content of reproductive male and female cisco and lake whitefish as proportions of carcass and viscera energy content of nonreproductive cisco and lake whitefish at the end of October. Values are after spawning for females and before spawning for males. Symbols as in Fig. 5.

cera energy reserves (64% for lake whitefish compared with 47% for male cisco) and a comparable proportion of their carcass energy reserves.

As in cisco, nonreproductive lake whitefish reached significantly higher carcass and viscera energy levels by October (Fig. 4). The carcass energy content of reproductive female lake whitefish after spawning was only 75% of the carcass energy content of nonreproductive fish (Fig. 6). Viscera energy content was also lower representing 33% of the viscera energy content of nonreproductive fish (Fig. 6) Compared with female cisco, the proportional loss of carcass and viscera energy of reproductive fish compared with nonreproductive fish was smaller for lake whitefish. The carcass energy content of reproductive female cisco represented 58% of the carcass energy content of nonreproductive females and viscera energy content only 17% of the viscera energy content of nonreproductive females. Comparisons for males before spawning also demonstrated a higher proportional loss of carcass and viscera energy of cisco in reproductive fish compared with nonreproductive fish (Fig. 6). However, the difference in the ratio of viscera energy of reproductive male on nonreproductive male was not significant between the two species.

During winter, reproductive fish of both species relied on their carcass energy reserves only whereas nonreproductive fish used both their carcass and viscera energy reserves (Fig. 3 and 4).

Proximate Composition

Gonads

While gonad fat and protein content of nonreproductive fish remained quite stable, gonad fat and protein content of reproductive fish increased significantly from May to October (Table 2). In reproductive females of both species, fat and protein con-

TABLE 2. Proximate composition of the gonads of standard reproductive (REP) and nonreproductive (NRP) cisco and lake whitefish from May 1982 to May 1983. Numbers in parentheses indicate standard errors.

Gonads			1982 May	July	Aug.	Sept.	Oct.	(mid) Nov.	1983 May
Cisco									
Percent moisture	Female	REP	72.7 (0.9)	66.6 (1.4)	59.3 (1.2)	58.7 (0.9)	61.4 (1.7)	84.7 (3.0)	83.8 (0.9)
		NRP	82.7 (2.3)	—	69.3 (1.6)	67.4 (1.7)	69.6 (1.2)	—	71.0 (1.3)
	Male	REP	77.7 (0.8)	79.5 (0.5)	79.2 (0.4)	72.0 (0.9)	77.8 (0.9)	—	77.6 (0.6)
		NRP	80.7 (0.8)	—	—	87.3 (6.2)	75.4 (0.4)	—	75.3 (0.8)
Fat content (g)	Female	REP	0.3 (0.1)	0.7 (0.1)	2.7 (0.2)	4.6 (2.1)	5.6 (0.3)	0.6 (0.1)	0.1 (0.1)
		NRP	0.1 (0.1)	—	0.3 (0.1)	0.4 (0.2)	0.4 (0.1)	—	0.2 (0.2)
	Male	REP	0.05 (0.02)	0.1 (0.1)	0.2 (0.1)	0.4 (0.1)	0.4 (0.3)	—	0.02 (0.02)
		NRP	0.04 (0.03)	—	—	0.05 (0.01)	0.04 (0.03)	—	0.01 (0.01)
Protein content (g)	Female	REP	0.3 (0.1)	0.6 (0.1)	2.2 (0.2)	4.9 (0.3)	7.1 (0.3)	0.4 (0.1)	0.2 (0.1)
		NRP	0.2 (0.1)	—	0.3 (0.1)	0.4 (0.1)	0.2 (0.1)	—	0.4 (0.1)
	Male	REP	0.1 (0.1)	0.4 (0.1)	0.5 (0.1)	1.0 (0.1)	0.5 (0.1)	—	0.1 (0.1)
		NRP	0.1 (0.1)	—	—	0.05 (0.04)	0.04 (0.02)	—	0.1 (0.1)
Lake Whitefish									
Percent moisture	Female	REP	82.3 (0.7)	66.4 (1.3)	61.2 (1.1)	—	60.6 (0.9)	84.3 (0.5)	85.2 (0.6)
		NRP	84.5 (0.8)	82.8 (0.2)	—	80.6 (0.8)	79.8 (0.6)	—	81.0 (0.8)
	Male	REP	82.0 (1.0)	79.8 (0.7)	77.8 (0.9)	72.5 (0.5)	72.9 (1.0)	81.8 (0.8)	81.0 (0.9)
		NRP	76.8 (2.4)	80.6 (0.2)	—	77.4 (0.2)	79.8 (0.6)	—	79.7 (0.7)
Fat content (g)	Female	REP	0.03 (0.02)	2.7 (0.3)	7.8 (2.2)	—	11.8 (0.7)	0.4 (0.2)	0.3 (0.1)
		NRP	0.1 (0.1)	0.02 (0.02)	—	0.1 (0.1)	0.1 (0.1)	—	0.4 (0.1)
	Male	REP	0.02 (0.02)	0.2 (0.1)	0.4 (0.1)	0.3 (0.1)	0.4 (0.1)	0.2 (0.2)	0.2 (0.1)
		NRP	0.04 (0.02)	0.04 (0.02)	—	0.05 (0.04)	0.1 (0.1)	—	0.1 (0.1)
Protein content (g)	Female	REP	0.3 (0.1)	3.4 (0.7)	10.8 (0.5)	—	16.1 (2.3)	1.0 (0.9)	0.4 (0.1)
		NRP	0.7 (0.1)	0.2 (0.1)	—	0.3 (0.1)	0.3 (0.1)	—	0.4 (0.1)
	Male	REP	0.1 (0.1)	1.2 (0.1)	1.9 (0.1)	1.0 (0.1)	1.2 (0.1)	0.3 (0.1)	0.1 (0.1)
		NRP	0.2 (0.1)	0.1 (0.1)	—	0.1 (0.1)	0.1 (0.1)	—	0.1 (0.1)

tent increased ($P<0.05$) during feeding (May to August) and freshwater migration (August and October). Conversely, percent moisture decreased ($P<0.05$) during the same period. After spawning (beginning of November) gonad fat and protein content decreased ($P<0.05$) and reached values similar to those of nonreproductive fish. In reproductive males of both species, the maximum fat and protein content of the testes were attained earlier than in females. In male cisco, maximum fat and protein content were reached at the end of September whereas in male lake whitefish maximum values were attained at the end of August (Table 2). In reproductive males of both species, protein content decreased ($P<0.05$) before spawning.

TABLE 3. Proximate composition of the carcass of standard reproductive (REP) and nonreproductive (NRP) cisco and lake whitefish from May 1982 to May 1983. Numbers in parentheses indicate standard errors.

Carcass			1982 May	July	Aug.	Sept.	Oct.	(mid) Nov.	1983 May
Cisco									
Percent moisture	Female	REP	69.0	69.3	68.9	74.0	74.8	79.0	75.6
			(0.7)	(1.0)	(0.6)	(2.4)	(0.6)	(0.1)	(0.5)
		NRP	73.5	—	69.4	69.7	69.8	—	70.4
			(1.7)		(0.6)	(0.8)	(0.3)		(0.3)
	Male	REP	70.8	67.4	68.3	70.3	74.0	—	76.2
			(1.2)	(0.9)	(0.5)	(1.6)	(0.3)		(0.3)
		NRP	73.6	—	—	71.3	68.3	—	69.7
			(0.7)			(0.7)	(0.9)		(0.8)
Fat content (g)	Female	REP	10.1	13.8	21.4	13.4	7.1	3.6	2.3
			(0.8)	(1.6)	(1.3)	(8.0)	(1.0)	(0.1)	(0.4)
		NRP	3.9	—	20.0	19.4	15.5	—	12.3
			(3.4)		(1.1)	(1.1)	(1.4)		(0.7)
	Male	REP	8.3	16.4	20.9	21.6	11.0	—	1.7
			(5.4)	(0.8)	(0.7)	(3.9)	(0.6)		(0.1)
		NRP	2.0	—	—	21.1	21.6	—	14.0
			(0.3)			(3.2)	(4.1)		(6.2)
Protein content (g)	Female	REP	30.7	38.7	41.3	36.5	33.5	35.2	27.1
			(1.0)	(1.1)	(1.6)	(2.8)	(1.9)	(2.9)	(0.9)
		NRP	23.4	—	42.9	45.4	41.4	—	37.3
			(2.2)		(1.2)	(1.2)	(0.9)		(1.3)
	Male	REP	31.7	41.2	39.2	43.4	39.3	—	25.8
			(0.9)	(1.1)	(2.8)	(1.6)	(1.9)		(1.2)
		NRP	24.2	—	—	40.9	45.2	—	36.0
			(1.1)			(0.7)	(2.3)		(1.0)
Lake Whitefish									
Percent moisture	Female	REP	69.9	67.0	71.3	—	75.1	74.0	74.5
			(0.5)	(0.6)	(1.0)		(0.7)	(0.6)	(0.7)
		NRP	73.4	71.5	—	71.5	71.4	—	69.7
			(1.3)	(1.3)		(1.0)	(0.7)		(0.5)
	Male	REP	70.3	67.7	72.0	73.8	72.9	73.7	74.9
			(0.6)	(0.5)	(0.5)	(0.7)	(0.3)	(0.6)	(0.5)
		NRP	74.5	70.8	—	71.9	71.5	—	72.2
			(1.2)	(0.1)		(0.7)	(0.4)		(0.6)
Fat content (g)	Female	REP	16.2	33.8	26.6	—	17.2	18.7	5.1
			(5.4)	(1.6)	(3.3)		(6.1)	(5.8)	(1.8)
		NRP	9.3	21.3	—	27.0	28.0	—	26.5
			(6.9)	(6.9)		(2.6)	(3.3)		(3.4)
	Male	REP	17.9	32.3	26.4	19.1	19.2	12.8	7.5
			(12.1)	(1.6)	(3.3)	(3.8)	(3.4)	(1.2)	(4.2)
		NRP	6.5	28.7	—	28.0	25.7	—	15.3
			(2.0)	(1.1)		(2.6)	(7.5)		(5.8)
Protein content (g)	Female	REP	59.2	86.6	74.9	—	70.6	73.7	51.6
			(2.5)	(5.2)	(7.1)		(1.7)	(3.4)	(4.5)
		NRP	59.0	64.8	—	76.3	76.5	—	68.5
			(3.1)	(6.1)		(3.8)	(6.4)		(4.9)
	Male	REP	67.9	80.8	81.2	80.2	82.0	74.0	43.9
			(1.9)	(3.8)	(6.2)	(1.1)	(1.9)	(2.1)	(2.9)
		NRP	63.7	82.0	—	84.1	89.9	—	70.6

Carcass

Carcass fat and protein increased ($P<0.05$) during the season for nonreproductive male and female cisco with peaks at the end or near the end of October (Table 3). In reproductive female cisco, carcass fat and protein reached their maximum values in August prior to river entry. During freshwater migration, both carcass fat and protein were utilized. However, fat represented 83% of the carcass energy reserves that were used. As a result of the extensive use of carcass fat for gonad maturation and migration, carcass protein was the main source of energy for the overwintering period for reproductive females, representing 94% of the somatic energy reserves that were used.

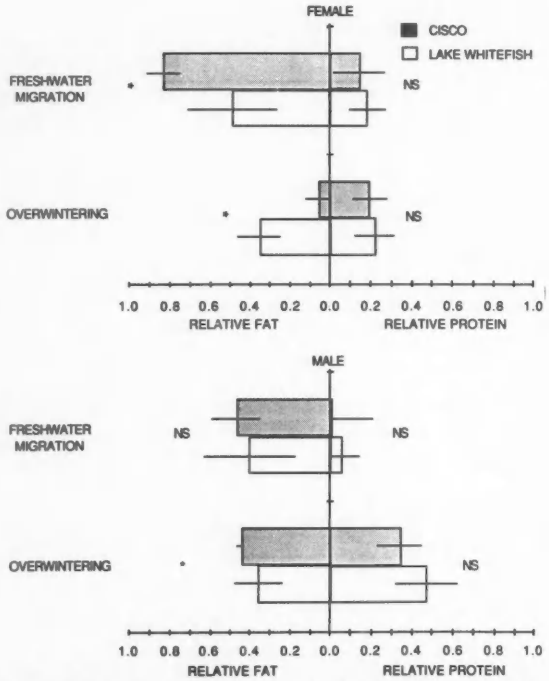

FIG. 7. Relative carcass lipid and protein decrease for cisco and lake whitefish during freshwater migration (after spawning for females and before spawning for males) and overwintering. Significant differences between the two species are indicated by an asterisk (Mann–Whitney U-test; $P<0.05$).

In nonreproductive females carcass fat and protein were utilised to the same extent during the overwintering period. The decline in energy produced by the decrease of carcass fat represented 53% of the carcass energy loss for nonreproductive females.

In reproductive male cisco, only carcass fat was used during freshwater migration, carcass protein content remaining almost constant during the same period (Table 3). By the following spring, both carcass fat and protein had decreased ($P<0.05$). Nonreproductive males also used both carcass fat (58% of the carcass energy loss) and protein during the overwintering period.

In nonreproductive lake whitefish, carcass fat and protein increased ($P<0.05$) from May to October, In reproductive females, the maximum levels of fat and protein were reached in July and decreased ($P<0.05$) during gonad maturation, freshwater migration and spawning (Table 3). Carcass fat represented 66% of the carcass energy reserves that were used. However, no differences ($P<0.05$) in carcass protein content were observed between reproductive and nonreproductive females in October. Conversely, the carcass fat level of reproductive females was lower ($P<0.05$) than that of nonreproductive females. During the overwintering period, carcass fat and protein were used by both reproductive and nonreproductive females.

In reproductive male lake whitefish, carcass protein content did not change ($P>0.05$) during gonad maturation and freshwater migration but decreased ($P<0.05$) during spawning (Table 3). Carcass fat decreased ($P<0.05$) during freshwater migration and spawning. Carcass fat and protein levels in reproductive males after spawning were lower ($P<0.05$) than in nonreproductive males. Like females, reproductive and nonreproductive males used both carcass fat and protein during the winter.

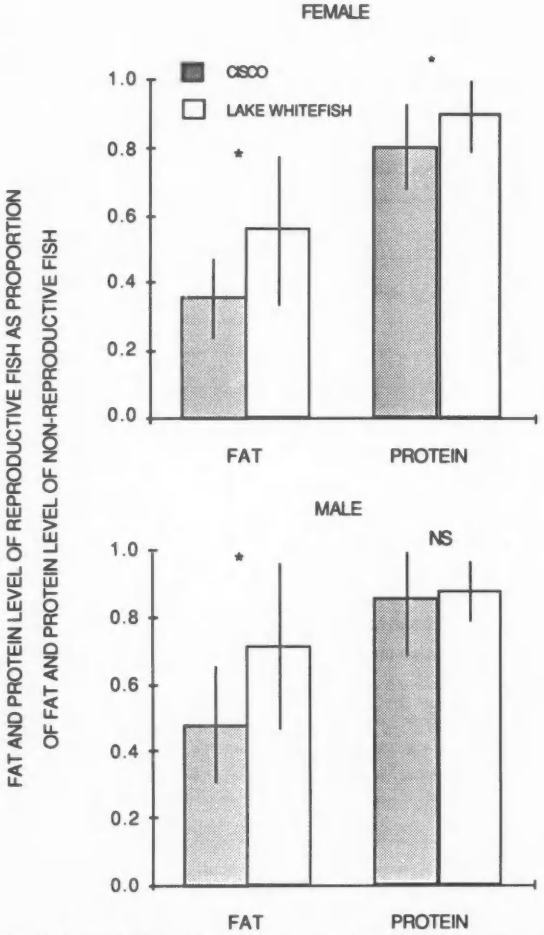

FIG. 8. Carcass lipid and protein content of reproductive male and female cisco and lake whitefish as proportions of carcass lipid and protein content of nonreproductive cisco and lake whitefish at the end of October. Values are after spawning for females and before spawning for males. Symbols as in Fig. 7.

Interspecific comparisons indicate that female lake whitefish used a smaller proportion of their carcass fat reserves than female cisco during migration and reproduction (Fig. 7). Female lake whitefish used 49% of their carcass fat reserves compared with 83% for female cisco. As a consequence, reproductive female lake whitefish still had carcass fat reserves that could be used during winter. Carcass fat decreased by 36% during winter in lake whitefish whereas in cisco, carcass fat reserves decreased by only 6% (Fig. 7). Compared with nonreproductive females, the depletion in carcass fat and protein after spawning was less acute for female lake whitefish than for female cisco (Fig. 8). Carcass fat and protein content of reproductive females as a proportion of carcass fat and protein content of nonreproductive females were significantly lower for cisco (Fig. 8).

No significant differences in carcass fat and protein used during freshwater migration were observed between male cisco and

TABLE 4. Proximate composition of the viscera of standard reproductive (REP) and nonreproductive (NRP) cisco and lake whitefish from May 1982 to May 1983. Numbers in parenthesis indicate standard errors.

Viscera			1982 May	July	Aug.	Sept.	Oct.	(mid) Nov.	1983 May
Cisco									
Percent moisture	Female	REP	71.5 (1.2)	71.3 (2.0)	68.7 (1.5)	74.8 (1.7)	78.9 (0.6)	82.4 (0.8)	78.9 (0.8)
		NRP	77.9 (2.2)	—	64.8 (2.1)	64.2 (1.9)	64.3 (3.7)	—	77.4 (5.8)
	Male	REP	75.8 (2.4)	66.1 (1.7)	62.6 (1.8)	64.6 (4.0)	70.2 (0.7)	—	79.2 (0.5)
		NRP	81.2 (0.5)	—	—	67.3 (7.0)	55.6 (7.5)	—	62.8 (2.9)
Fat content (g)	Female	REP	0.9 (0.1)	1.5 (0.2)	1.6 (0.8)	0.6 (0.4)	0.3 (0.2)	0.2 (0.1)	0.1 (0.1)
		NRP	0.3 (0.2)	—	1.0 (0.2)	2.3 (0.9)	2.1 (0.3)	—	0.9 (0.3)
	Male	REP	0.3 (0.1)	2.1 (0.2)	1.9 (0.4)	2.1 (1.8)	0.7 (0.1)	—	0.02 (0.02)
		NRP	0.3 (0.2)	—	—	3.0 (2.0)	4.6 (1.1)	—	1.3 (1.0)
Protein content (g)	Female	REP	1.2 (0.1)	1.3 (0.1)	1.4 (0.1)	1.4 (0.1)	0.9 (0.1)	0.7 (0.1)	1.0 (0.1)
		NRP	1.3 (0.3)	—	1.3 (0.3)	2.2 (0.5)	1.7 (0.2)	—	1.6 (0.5)
	Male	REP	1.1 (0.1)	1.2 (0.1)	1.3 (0.3)	1.2 (0.1)	0.9 (0.1)	—	1.1 (0.1)
		NRP	1.0 (0.1)	—	—	1.9 (0.2)	1.6 (0.7)	—	1.5 (0.4)
Lake Whitefish									
Percent moisture	Female	REP	76.3 (0.6)	67.7 (6.3)	65.0 (4.0)	—	79.3 (0.7)	78.6 (0.4)	79.0 (0.4)
		NRP	79.0 (1.4)	69.7 (2.4)	—	60.8 (3.8)	59.6 (3.3)	—	70.7 (1.1)
	Male	REP	75.1 (3.7)	68.4 (1.4)	70.2 (0.8)	79.2 (0.8)	77.6 (0.8)	78.3 (0.7)	79.3 (0.4)
		NRP	80.5 (1.0)	68.4 (2.0)	—	70.6 (1.8)	64.6 (1.9)	—	75.0 (1.5)
Fat content (g)	Female	REP	1.7 (0.9)	9.0 (4.2)	4.1 (3.4)	—	1.1 (0.7)	0.6 (0.5)	0.3 (0.1)
		NRP	0.7 (0.6)	4.6 (0.7)	—	4.7 (1.0)	5.9 (0.8)	—	2.8 (0.7)
	Male	REP	1.7 (1.2)	5.9 (3.3)	3.7 (0.6)	2.0 (1.8)	1.2 (0.9)	0.9 (0.8)	0.3 (0.2)
		NRP	0.9 (0.7)	4.4 (0.4)	—	3.8 (1.8)	4.0 (1.0)	—	1.3 (1.1)
Protein content (g)	Female	REP	4.4 (0.3)	6.3 (0.8)	5.3 (0.5)	—	2.9 (0.2)	3.8 (0.3)	4.8 (0.2)
		NRP	4.1 (0.5)	5.8 (0.6)	—	4.3 (0.4)	4.7 (0.3)	—	4.2 (0.2)
	Male	REP	4.2 (0.3)	5.9 (0.3)	4.9 (0.4)	4.1 (0.1)	3.0 (0.2)	3.1 (0.2)	4.6 (0.2)
		NRP	3.6 (0.3)	4.2 (0.2)	—	7.5 (1.0)	3.9 (1.0)	—	4.9 (0.3)

lake whitefish (Fig. 7). However, during the period covering spawning and overwintering, carcass fat reserves declined to a greater extent in male cisco (Fig. 7). Carcass fat reserves of reproductive male cisco as a proportion of carcass fat reserves of nonreproductive male cisco were also significantly lower than in male lake whitefish (Fig. 8).

In both species, significant variations in percent moisture of the carcass were observed. Changes in percent moisture were the inverse of changes in carcass fat and protein levels (Table 3).

Viscera

In reproductive cisco, both viscera fat and protein were used during the freshwater migration (Table 4). Reproductive females used 90% of their viscera fat and 63% of their viscera protein. In reproductive males, these percentages were lower (64% of viscera fat and 27% of viscera protein) but these values are probably underestimated. As a consequence, viscera fat and protein content of reproductive cisco were lower ($P<0.05$) than in nonreproductive cisco at the end of October except for viscera protein content of reproductive and nonreproductive male cisco. The viscera fat content of nonreproductive cisco is used to cover a part of the energy demands of overwintering while viscera protein did not vary significantly (Table 4). In reproductive cisco, slight changes in viscera fat and protein content

TABLE 5. Energy gain, reproductive effort, somatic cost of reproduction, and overwintering cost for male and female cisco and lake whitefish. For the definition of terms see text.

Total and somatic energy gain		Cisco		Lake Whitefish	
		Female	Male	Female	Male
l_n	(kJ)	1273.	1471.	1566.	1608.
l_s	(kJ)	−271.	<218.	166.	−48.
l_r	(kJ)	1144.	>469.	1747.	1274.
l_a	(kJ)	873.	688.	1912.	1226.
R_a	(kJ)	−401.	−784.	346.	−382.
Reproductive effort and somatic cost					
R_e	(%)	58.	>25.	44.	35.
	(kJ/kg)	3727.	>1597.	2885.	2008.
R_s	(kJ)	1544.	>1253.	1401.	1656.
RE_s	(%)	121.	>85.	89.	103.
Overwintering cost					
TEC_r	(%)	67.	63.	64.	61.
W_a	(%)	9.	—	20.	26.
W_n	(%)	26.	32.	12.	27.

TABLE 6. Relative importance of energy investment in migration and migration effort for male and female cisco and lake whitefish. MG represents the energy loss for migration between August and October for cisco and between July and October for lake whitefish. Mg representing the energy loss for migration between August and October for lake whitefish was also calculated in order to compare the two species for the period during which fish ascend the rapids. MG_e and Mg_e are calculated from the corresponding MG and Mg values.

Relative importance of migration		Cisco		Lake Whitefish	
		Female	Male	Female	Male
MG	(kJ)	585.	450.	883.	731.
Mg	(kJ)			557.	467.
MG/l_g		1.64	22.78	1.02	12.99
MG/l_{gm}		2.70	75.53	1.30	146.07
Migration effort					
MG_e	(%)	29.	24.	22.	20.
	(kJ/kg)	1907.	1530.	1459.	1153.
Mg_e	(%)			14.	13.
	(kJ/kg)			940.	745.

between November and May were observed but these variations were not significant.

In lake whitefish, viscera fat and protein were also used extensively by reproductive individuals during gonad maturation and migration (Table 4). Male and female lake whitefish used 85 and 93% of their viscera fat, respectively and 47 and 39% of the viscera protein, respectively. By the end of October, viscera fat and protein content were lower in reproductive fish compared with nonreproductive ones ($P<0.05$) except for viscera protein content of male lake whitefish. As in cisco, nonreproductive lake whitefish used their viscera fat reserves to cover part of the energy cost of overwintering. The decrease in viscera fat represents 91 to 100% of the viscera energy loss during overwintering. Viscera protein content did not change during that period. In reproductive lake whitefish, changes in viscera fat and protein during the winter were not significant. The changes in percent moisture of viscera for cisco and lake whitefish were the inverse of changes in viscera fat and protein.

Reproductive Effort and Somatic Cost of Reproduction

Differences in total energy gain and somatic energy increase between reproductive (l_a, l_s) and nonreproductive (l_n) cisco and lake whitefish were observed (Table 5). The somatic energy increase of nonreproductive fish (l_n; equivalent to total energy gain) was higher than the total energy gain of reproductive fish (l_a) except for female lake whitefish where somatic energy increase of nonreproductive females was lower than total energy gain of reproductive females.

Reproductive effort (R_e) indicates that the energy investment in reproduction by female cisco represented 58% of their somatic energy content and for males, 25% of their somatic energy content (Table 5). In male cisco, however, reproductive effort was underestimated because the energy cost of spawning activities could not be estimated. In lake whitefish, the energy invested in reproduction represented 44% (female) and 35% (male) of their somatic energy content.

On a comparative basis, reproductive effort in female cisco was higher than male and female lake whitefish. Female cisco allocated more energy to reproduction (l_r) than their total energy gain (l_a) whereas in lake whitefish the energy invested in reproduction was less or almost equal to the total energy gain during the season.

The energy investment in reproduction (l_r) in all cases was higher than the difference in total energy gain between reproductive and nonreproductive fish (R_a). Therefore, energy investment in reproduction was at the cost of somatic energy increase (Table 5). The somatic cost of reproduction indicates that somatic energy increase of reproductive fish was in all cases lower than the somatic energy increase of nonreproductive fish. Expressed in relative terms (RE_s), reproduction of female cisco resulted in a reduction of somatic energy increase equal to 121% of the somatic energy increase of nonreproductive fish (Table 5). In the case of female lake whitefish, reproduction reduced somatic energy increase by 89% of the somatic energy increase of nonreproductive fish.

Considering the energy cost of overwintering, reproductive males and females of both species consumed 61 and 67% of the somatic energy content they reached before migration to meet the energy demands of reproduction and overwintering (TEC_r, Table 5). The energy loss during winter was lower for reproductive female cisco (W_a) than for nonreproductive female cisco (W_n). In lake whitefish, the energy loss during winter of reproductive and nonreproductive individuals was comparable.

Cost of Migration

During the freshwater migration of both species, the energy cost of migration was higher than the energy invested in gonads and higher in female cisco than in female lake whitefish (MG/I_{gm}, Table 6). In males of both cisco and lake whitefish, the energy cost of migration was almost the only cost of reproduction representing respectively 76 and 146 times more energy than the energy invested in the testes.

The energy cost of migration was higher than the total energy investment in the gonads (164%) for female cisco and equal to the total energy investment in the gonads (102%) for female lake whitefish (MG/I_g, Table 6). The energy cost of migration represented 20 to 29% of the somatic energy content of reproductive fish of both species. The migratory effort (MG_e) also indicates that cisco expended more energy for migration than

lake whitefish, the difference between males and between females being respectively 17 and 24%. This difference is even larger if we consider the same period of time (August to October), the period during which fish ascended the rapids and moved to the spawning grounds. During this period of time, cisco expended two times more energy for migration than lake whitefish (Table 6). On an equivalent weight basis the results are the same.

Discussion

Differences in seasonal energy increase between reproductive and nonreproductive cisco and lake whitefish, as well as energy expenditures associated with reproduction, result in somatic loss for reproductive fish of both species (Table 5). However, the somatic depletion for reproduction is higher in cisco than in lake whitefish. Migration alone appears responsible for the higher somatic depletion for reproduction in cisco (Table 6).

Energy Allocation to Growth and Reproduction

Resource input

No significant differences in the increment in length between reproductive and nonreproductive fish were observed for cisco and lake whitefish suggesting that nonreproductive fish do not devote more energy than reproductive fish to growth in length (Table 1). In the laboratory, the length of guppies (*Poecilia reticulata*) did not differ significantly between reproducing and nonreproducing fish but nonreproducing females had significantly more energy in their somatic tissues than reproducing females (Reznick 1983). However, other workers have demonstrated significant differences in growth between reproductive and nonreproductive fish. For example, in male bluegill sunfish, Gross and Charnov (1980) estimated that within an age group, males with mature testes had a significantly smaller linear growth increment than equal-aged males with immature testes, in the season they were captured. These differences were explained by two distinct reproductive pathways, cuckoldry and parental strategy. Hirshfield (1980) observed that reproduction and growth of the Japanese medaka (*Oryzias latipes*) were in general negatively correlated suggesting that individuals reproducing the most were not able to grow as rapidly as individuals reproducing less. In these studies however, alternative reproductive strategies were implied as opposed to one reproductive strategy where years of reproduction alternate with years of nonreproduction.

The significantly higher energy content of nonreproductive cisco and lake whitefish in October (Fig. 2), due to the fact that no energy was allocated to reproduction, indicates that surplus energy was devoted to energy storage, as opposed to increase in length. By calculating the energy increase in nonreproductive fish if no growth had occurred between May and October, we estimated that 65% (52 and 72%) of the total energy gain in nonreproductive fish during that period was due to energy storage. The remaining 35% was due to growth. Energy content estimated for juvenile fish (Y. Lambert, unpubl. data) indicated that 27% (23 to 38%) of the total seasonal energy increase was due to storage. Thus growth was responsible for most of the energy increase (73%) in juvenile fish. As juveniles, fish grow in length and energy and as they approach the age of maturity more energy is accumulated as energy reserves to the detriment of growth.

As fish reach maturity, differences in total energy gain are observed. The total energy gain of reproductive fish is lower than the somatic energy gain of nonreproductive fish except for female lake whitefish which exhibited the opposite pattern (Table 5). Thus, reproduction appears in most cases to reduce energy gain during the summer. This may be related to the fact that reproductive individuals leave the feeding grounds in August to move to the river while nonreproductive fish stay on the feeding grounds until September. Although some reproductive lake whitefish captured in the estuarine portion of the freshwater migration had food in their stomachs (Dodson et al. 1985), it does not appear that feeding reduces greatly the energy lost during the freshwater migration. This could be the result of lower food availability in the river and/or lower intensity of feeding. The cost of migration per unit of distance (42.8 $kJ \cdot kg^{-1} \cdot km^{-1}$) for lake whitefish in relation to the relative migration distance in body lengths ($9 \cdot 10^4$) and weight (0.625 kg) is within the range of other anadromous species that stop feeding during migration (Bernatchez and Dodson 1987). This suggests that feeding in lake whitefish during the estuarine part of the migration is not energetically important. However, reproductive female lake whitefish show a higher resource input than nonreproductive females. This difference seems related to a higher intensity of feeding between May and July. The energy increase during this period is higher in reproductive females than in nonreproductive females and males (Fig. 2). Dabrowski (1982b), reporting data of Szypula (1965) indicated that the feeding intensity of female vendace (*Coregonus albula* L.) was greater than that of males during gonad maturation.

During freshwater migration cisco and lake whitefish rely mostly on their energy reserves as they stop feeding before or soon after river entry. Even if cisco and lake whitefish move to the spawning grounds at the same time (Dodson et al. 1985), the maximum somatic energy content before migration is observed sooner in lake whitefish than in cisco (Fig. 2). Sampling interval and difference in energy increase in gonads can partly explain this difference. Because of the 1-mo interval between the July and August sampling dates, a difference of up to 4 wk in time of arrival of the two species at the river mouth is possible. If lake whitefish move to the river mouth earlier than cisco, as suggested by the data of 1979 to 1981 (Lambert and Dodson 1982a,b), the energy costs associated with entry into freshwater would be observed earlier in lake whitefish than in cisco. These costs include physiological changes associated with osmoregulation and a higher standard metabolism associated with the higher water temperatures in the river than in the bay (Dodson et al. 1985). The higher rate of displacement in the river of cisco (Dodson et al. 1985) suggests that cisco move later to the river mouth and migrate more rapidly than lake whitefish explaining why the two species are observed together during the upriver migration. The greater energy increase in gonads in lake whitefish by the end of August may also be partly responsible for the earlier decrease in energy because of energy transfer to the gonads.

Resource expenditures

Both carcass and viscera energy reserves are used during freshwater migration (Fig. 3 and 4). However, more than 75% of the total energy expenditures for migration and reproduction come from the utilization of carcass energy reserves. Dabrowski (1982a,b) observed that in vendace (*Coregonus albula* L.) and pollan (*Coregonus pollan* Thompson) muscle was the principal source of energy for gonad maturation. Both carcass fat and

protein decreased during freshwater migration (Table 3) but the comparison between males and females suggests that the decrease in carcass protein is mainly associated with gonad maturation. The decrease in carcass fat is associated with both gonad maturation and migration in females and almost exclusively with migration in males. Male cisco and lake whitefish deposit little energy in their testes (less than 6 kJ) during freshwater migration suggesting that most energy lost during that period is associated with migration. For males, no significant decrease in carcass protein occurs before spawning (Table 3) suggesting that carcass fat is the principal source of energy for migration in males. In females of both species, decrease in carcass protein is associated primarily with gonad maturation as gonad protein increase represents 80% of the carcass protein decrease. This result is consistent with the study of Dabrowski (1982a) who showed that the decrease in different amino acids in the muscle of pollan (*Coregonus pollan* Thompson) was closely related to their increase in gonads. The decrease in carcass fat for females may be associated with both gonad maturation and migration resulting in a higher carcass fat decrease in females than in males (Table 3).

Viscera energy reserves, although less important than carcass energy reserves, contribute 7% of the energy used during freshwater migration for cisco and 20% for lake whitefish. Reproductive fish use a large proportion of their viscera fat and protein during freshwater migration (Table 4). As a consequence, they rely mostly on their carcass energy reserves during winter. In contrast, nonreproductive fish derived 19 to 33% of the energy they need to overwinter from their viscera energy reserves, principally in the form of fat, thus reducing their loss of carcass reserves during the winter. The difference in the viscera energy reserves used during the winter supports the proposition that the stress of overwintering will be greater in reproductive fish because their carcass reserves, already lower than those of nonreproductive fish, will be reduced to an even greater extent during winter.

The large use of viscera fat and protein in migration and reproduction results in visceral atrophy. The atrophy of the digestive system in known to result in a lower efficiency of digestion since it increases gastric retention times (Jobling 1980) and reduces the ability to synthesize and secrete digestive enzymes (Windell 1966). In contrast, nonreproductive fish use only their viscera fat reserves which are accumulated around the digestive system and no atrophy is observed.

The large energy depletion associated with reproduction and overwintering (Fig. 2) suggests that surviving fish that reproduce one year must skip at least the next reproductive season in order to accumulate sufficient energy reserves to spawn again. Following the overwintering period, surviving cisco and lake whitefish that spawned the previous fall have 50% less energy (48 to 57%) than fish that did not spawn. Moreover reproductive fish have less energy in May 1983 after spawning and overwintering than in the previous spring (Fig. 2). The difference in energy content between reproductive and nonreproductive individuals could even be larger as the energy cost of overwintering is probably underestimated because of selective mortality, with fish in the poorest condition suffering the greatest mortality. The similarity between the total energy loss for reproduction and overwintering in cisco and lake whitefish can be attributed to such a bias in the determination of the cost of overwintering in reproductive fish. It may be assumed that the energy cost of overwintering would be comparable between reproductive and nonreproductive fish if they were equally vulnerable to mortality. Applying the energy cost of overwintering of nonreproductive female cisco to reproductive female cisco, we obtain a higher total energy loss for reproduction and overwintering for female cisco (in the order of 84%) than that observed (67%). In the case of lake whitefish, a similar calculation produces values of total energy loss (62% for males and 57% for females) comparable with the total energy loss for reproduction and overwintering observed (61 and 64%, Table 5). The difference, at least in female cisco, would indicate a greater mortality of reproductive females relative to nonreproductive females with only spent fish in the best condition surviving the winter. In lake whitefish we would expect little or no difference in mortality between reproductive and nonreproductive fish if the energy cost of overwintering is comparable for the two groups.

Reshetnikov et al. (1970) concluded that in whitefish (*Coregonus lavaretus* L.) of Lake Chun in USSR, maturation of the gonads was not only dependent on the attainment of a definite size and age but also on the attainment of a definite level of fat reserves specific to each population. Assuming a minimum energy level for maturation of James Bay coregonines, fish that spawn must accumulate energy reserves the following season and sacrifice growth. Given the short period for feeding (less than 3 mo), it seems very difficult if not impossible for a fish to spawn in consecutive years. Fish skipping the next opportunity to spawn would then benefit from a longer feeding period during which they would accumulate sufficient energy reserves for the next spawning season.

Although having a similar gonad energy content in May (Fig. 3 and 4) gonad development is very different between reproductive and nonreproductive females. In females that spawned the previous fall, gonads have a flaccid appearance, still contain unresorbed eggs and have a high moisture content (Table 2). Females that did not spawn have a lower moisture content and show a more advanced maturity stage (Nikolskii's (1963) stage III) suggesting that the maturation process had already begun. This also supports the conclusion that cisco and lake whitefish spawning one year must skip at least the following spawning season. Kuklin (1979) showed that muksun (*Coregonus muksun*) of the Yenisey River in northern USSR were unable to spawn annually and that length of the maturation process could be responsible. In fish presenting characteristic signs of the postspawning state (flaccid appearance of ovaries, unresorbed eggs), he estimated that the period of rematuration should last no less than 1.5 yr, making yearly spawning impossible. This long period of rematuration was associated with ecological conditions and the physiological state of fish. In James Bay, the low energy stores in reproductive cisco and lake whitefish after spawning (Fig. 2) may prevent the resorption of the gonads before spring and thus retard the rematuration process.

Several studies of northern populations of Arctic charr, brook charr, lake trout, cisco, and lake whitefish also report that fishes intermittently skipped reproduction (Kennedy 1949, 1953; Sprules 1952; Johnson 1972, 1980; Dutil and Power 1980; Morin et al. 1982). Dutil (1982, 1986) using energy content analysis, demonstrated that anadromous Arctic charr in the Northwest Territories were unable to spawn every year and could skip more than 2 yr between reproductive events. He observed that in spring, postspawners had about 46% less energy than maturing fish which is very comparable with the values we observed for cisco and lake whitefish. In all these studies, the restricted energy budget caused by short growing seasons seems to be one of the major factors limiting the pos-

sibilities of reproduction. Bull and Shine (1979) reporting data on amphibians, reptiles, and fishes, also concluded that lower frequency of reproduction (once every two or more years) was found in habitats of low quality or short growing seasons. They also noted that such situations are often characterized by a major accessory activity associated with reproduction such as migration, egg brooding, or live bearing.

Somatic cost of reproduction

The energy invested in reproduction (I_r) is high in both cisco and lake whitefish (Table 5) being almost equal to or higher than the total energy gain (I_a) of reproductive fish. Reproductive effort in both cisco and lake whitefish produced somatic cost (Table 5) such that the energy invested in reproduction reduced the somatic energy gain that would have been expected if fish had not reproduced. The trade-off in energy allocation between reproduction and other functions in cisco and lake whitefish is clearly shown by comparing reproductive and nonreproductive fish. Our results demonstrate that energy gain in nonreproductive fish is higher than in reproductive fish for males and females of both species with the exception of female lake whitefish which exhibited the opposite pattern.

Somatic energy increase of nonreproductive fish could be biased by the fact that individuals classified as nonreproductive fish between July and November include repeat spawners missing an opportunity to spawn and late maturing virgin fish that never spawned. However, if the energy content of repeat spawners and late maturing virgin fish were very different, we would expect much larger variance in the energy content of individuals classified as nonreproductive fish in October. However, within the standard errors of energy content and mean increase in length for nonreproductive individuals, the estimations of the somatic cost of reproduction for the two species changed by only 1 to 3%. Although comparable in their energy content in October, repeat spawners and late maturing virgin fish could nevertheless show differences in their seasonal pattern of growth and energy storage.

Relative Importance of the Energy Cost of Migration

Migration incured somatic costs in both species and was largely responsible for the higher somatic cost of reproduction in cisco. In females of both species, the proportion of the total energy gain invested in gonads is comparable (41% for cisco; 45%, lake whitefish). Migration resulted in somatic cost in two ways. As already mentioned, reproductive fish migrate to the river several months before nonreproductive fish. Thus, the reproductive migration reduced feeding. In the case of female lake whitefish, reproductive fish exhibit greater energy gain than nonreproductive fish despite their early departure from the feeding grounds. Thus, the lower somatic cost of reproduction in female lake whitefish is partly due to their ability to accumulate reserves in excess of nonreproductive fish prior to migration.

Migration also results in somatic cost due to the cost of displacement in freshwater. The energy loss for migration as a proportion of the somatic energy content before freshwater migration (MG_a) is higher in cisco and twice as high in cisco than in lake whitefish if we consider only the period during which fish ascend the rapids and move to the spawning grounds.

The difference in energy expenditure associated with swimming activity represents one of the major factors explaining the higher energy cost of migration for cisco. At low swimming speeds (29 to 35 $cm \cdot s^{-1}$ which is equivalent to 0.9 to 1.2 body lengths$\cdot s^{-1}$) the energy expenditures (joules per kilogram per hour) for standard metabolism and swimming activity are comparable between "standard" cisco and lake whitefish (Bernatchez and Dodson 1985). However, at higher swimming speeds energy expenditures increase more rapidly in cisco than in lake whitefish. At a swimming speed of 40 $cm \cdot s^{-1}$, the energy expenditure of cisco is 1.12 times higher than in lake whitefish. At 70 $cm \cdot s^{-1}$ the energy expenditure of cisco is 2.2 times higher and at 80 $cm \cdot s^{-1}$, 2.7 times higher. Correcting for differences in body weight, cisco swimming at 40 $cm \cdot s^{-1}$ would expend 0.9 times the energy expended by lake whitefish but at speeds of 70 to 80 $cm \cdot s^{-1}$, the energy expended by cisco would be 1.7 to 2.1 times greater than that of lake whitefish. The high sustained swimming speeds needed to ascend the 7 km of rapids in the Eastmain River where current velocities vary from 0.7 to 1.5 $m \cdot s^{-1}$ will necessarily result in a higher energy expense in cisco. This conclusion is supported by the fact that metabolic adjustments to increase the aerobic capacity of the swimming musculature are more dramatic for cisco compared with lake whitefish in the Eastmain River (Guderley et al. 1986). The smaller size of cisco will also increase the energy cost of migration. Glebe and Leggett (1981) demonstrated in American shad (*Alosa sapidissima*) a higher energy cost of migration in smaller fish.

These results demonstrate that an energy cost is associated with reproduction for both cisco and lake whitefish in the Eastmain River and that the energy cost of migration is mostly responsible for the different somatic costs of reproduction observed between the two species. The energy cost of migration is important in determining the reproductive pattern of both species and results in differences in the life history characteristics exhibited by the two species (Lambert and Dodson 1989).

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Influence of Freshwater Migration on the Reproductive Patterns of Anadromous Populations of Cisco (*Coregonus artedii*) and Lake Whitefish (*C. clupeaformis*)[1]

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We tested the hypothesis that differences in the cost of freshwater migration are responsible for the different reproductive patterns exhibited by the Eastmain River (James Bay) populations of anadromous cisco and lake whitefish, as predicted by species-specific migration costs that result in interspecific differences in energy allocation to growth, survival, and reproduction. In the Eastmain River, cisco spawn at a younger age and a smaller size, have a shorter life span and show a higher fecundity and a higher mortality than lake whitefish. Assuming that the two populations are stable (being only lightly exploited), the two species spawn at an age that maximizes their lifetime fecundity. Either juvenile (between three and age at maturity) and/or adult mortality is of major importance in moulding the observed age at maturity but adult mortality may play a predominant role. Adult mortality is associated with migration, an obligatory cost representing a major proportion of the energy loss experienced by reproductive individuals. The difference in the energy cost of migration between the two species suggests that migration may play a predominant role in producing the different reproductive patterns of cisco and lake whitefish in the Eastmain River and that within the physiological and size constraints of each species. these patterns represent optimal adaptations maximizing fitness.

Nous avons testé l'hypothèse selon laquelle les différences dans le coût de la migration en eau douce étaient responsables des différences dans les patrons de reproduction observés chez les populations anadromes du cisco et du grand corégone de la rivière Eastmain (Baie James), comme prédit par les coûts de migration spécifiques à chaque espèce résultant en des différences inter-spécifiques dans la répartition de l'énergie entre la croissance, la reproduction et la survie. Dans la rivière Eastmain, le cisco se reproduit à un plus jeune âge et à une taille plus faible, a une durée de vie plus courte et montre une fécondité relative et une mortalité plus élevées. En supposant que les deux populations sont stables, les deux espèces se reproduisent à une âge où la fécondité totale pendant leur vie est maximisée. Les mortalités juvénile (≥3 ans) et adulte ont une influence importante sur l'âge à la maturité sexuelle mais la mortalité adulte pourrait jouer un rôle prédominant. La mortalité adulte est associée à la migration. Le coût obligatoire de la migration représente une proportion importante des dépenses énergétiques encourues par les poissons reproducteurs des deux espèces. La différence dans le coût énergétique de la migration entre les deux espèces suggère le rôle important de la migration dans la production de patrons de reproduction différents entre le cisco et le grand corégone de la rivière Eastmain et montrent qu'en fonction des différences physiologiques et de taille entre les deux espèces, les patrons de reproduction observés représentent des adaptations optimales.

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The differential reproductive success of species living in a particular environment can produce a great diversity of reproductive patterns, each of them presumably maximizing the individual's lifetime reproductive success (Pianka 1976). Schaffer (1974) suggested that related species with similar ecologies may have very different life histories, the differences resulting from historical accidents which trapped each species in a different adaptive peak.

Anadromous forms of cisco (*Coregonus artedii*) and lake whitefish (*C. clupeaformis*) provide a good opportunity to study the effect of the same environment on life history variables of similar species and to identify constraints which might explain differences in their life histories. Cisco and lake whitefish are found along the eastern coast of James and Hudson Bay. Both species represent a numerically important component of the fish communities of these regions (Morin et al. 1980; Lambert and Dodson 1982a,b; Kemp et al. 1989). These populations are assumed to be in stable equilibrium with their physical and biotic environment although subject to some exploitation by native subsistance fisheries (Morin et al. 1982) Natural selection should have molded the observed reproductive patterns so that each corresponds to a local optimum that maximizes the lifetime reproductive success of the individuals of each population. Cisco and lake whitefish are close phylogenetically and show in their natural range a large plasticity and considerable

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overlap in their life history characteristics (Jensen 1981, 1985; Scott and Crossman 1974). In the rivers of James and Hudson Bay, the two species exhibit differences in some life history characteristics. In the La Grande river, lake whitefish attain a greater maximum age, a greater size and a later age at sexual maturity whereas cisco exhibit a greater rate of growth prior to reproduction and a greater fecundity (Morin et al. 1982).

The general ecology of the two species is quite similar. Both species spawn at the base of rapids in La Grande River (Morin et al. 1981) and in the Eastmain River (Dodson et al. 1985). Lake whitefish spawn between mid and late October when water temperatures are approximately 5°C whereas cisco spawn on the same grounds 2 to 3 wk later just before freeze-up. Larvae of both species hatch the following spring and are flushed at spring breakup from the rivers into James Bay (Ochman and Dodson 1982). They return as juveniles in September and October and they overwinter in freshwater. The next spring, they leave freshwater for their feeding migration to James Bay. Adult fish exhibit different patterns of migration according to sexual maturity. Although iteroparous, adults of both species do not spawn every year (Morin et al. 1982; Dodson et al. 1985; Lambert and Dodson 1990). The upstream migration of the reproductive adults begins in mid to late July. After spawning, reproductive adults leave the spawning grounds and join nonreproductive adults and juveniles for the overwintering period in freshwater.

Migration is an essential component of the life cycle of cisco and lake whitefish and must be accounted for in evaluating the adaptive significance of the reproductive patterns for the two species. The energy cost of freshwater migration has a significant effect on reproductive effort and somatic loss due to reproduction for both species (Lambert and Dodson 1990). However, there is a higher cost of migration for cisco in the Eastmain River which in turn results in a higher somatic cost for cisco. As the energy investment in gonads is comparable for both species, the difference in the somatic cost of migration is the major factor responsible for the difference in the cost of reproduction between the two species (Lambert and Dodson 1990).

These results may be related to the more general idea of differential allocation of energy resources where the optimal combination of life history traits may be achieved by allocating energy among growth, maintenance and reproduction in a way that maximizes the individual's contribution to future genotypes (Cody 1966; Holgate 1967; Gadgil and Bossert 1970; Charnov and Krebs 1973; and Mountford 1973). This hypothesis of a trade-off in energy allocation implies that an increase in reproductive effort inevitably results in both an increase in current reproductive output and an increase in somatic cost that will reduce the probability of surviving to the next breeding season (survival cost) and/or reduce future reproductive output (Williams 1966; Gadgil and Bossert 1970). Bell (1980) for example, suggested that the degree of anadromy in salmonids, through its influence on adult survival, may affect the pattern of covariation in life histories. Schaffer and Elson (1975) examined variations in life history data among local populations of Atlantic salmon and found that the pattern of variation was correlated with the difficulty of migration; the mean age of first spawning increased with the difficulty of upstream migration as estimated by the distance the fish ascended into freshwater. Glebe and Leggett (1981) also demonstrated the relation between energy expenditures for migration and reproduction with semelparity and iteroparity along a latitudinal cline for the American shad (*Alosa sapidissima*).

In this study, we hypothesized that the higher cost of migration and higher somatic cost of reproduction in cisco, relative to lake whitefish, should result in different survival and fecundity costs and consequently in different species-specific reproductive patterns. The higher somatic cost of reproduction in cisco should be associated with a higher adult mortality, shorter life and an earlier age at maturity in cisco relative to lake whitefish. To examine the influence of migration on the reproductive patterns of the two species, the following aspects of their reproductive patterns were studied; age at maturity, growth, survival, and reproductive life span. Lifetime fecundity was used as the measure of fitness to estimate the optimal age at maturity of the two species.

Materials and Methods

Catch Analysis

Field work took place in the Eastmain River and adjacent areas from 1979 to 1981 using experimental gill-nets (Lambert and Dodson 1990). Variations in catch per unit of effort of gill-net samples were used to document the seasonal migration patterns of cisco and lake whitefish (Lambert and Dodson 1982b). The sampling area was divided into three regions (river, river mouth, and bay) and three periods (May to mid-June, mid-June to mid-August, and mid-August to October) corresponding to the major distributional pattern of fish. CPUE was estimated in each region for each period of time, the unit of effort being 24 h of fishing with one experimental gill-net. Although fish of one species can be in different regions according to their maturity stage and their age, no major movements between the regions occurred within each period of time. Considering the area sampled as the distributional area of the two populations, it was assumed that the sampling in the three regions during one period represented a discrete sampling of the whole population. For these reasons, the average CPUE of the different regions were summed for each period. A mean annual CPUE for each species was calculated with the values of the three periods and used as the observed CPUE of each species.

Each specimen sampled was measured (fork length) and weighed, maturity stage (Nikolskii 1963) and sex determined and otoliths taken. Gonad weight was also taken and for females, eggs were fixed in Gilson's fluid. Fecundity was estimated gravimetrically by the dry weight method (Bagenal 1978).

Life History Variables

Age determinations were made from otoliths, as scales underestimate the age of older fish (Morin et al. 1982; Power 1978). The otoliths were embedded, sanded on their sagittal section and immersed in glycerine to improve the contrast between the zones (Panella 1980). Two independent readings were made for each fish. In case of disagreement between the first two readings, a third was made to determine age. When the three readings gave different ages, otoliths for that fish were rejected. The agreement between the two readings was good for both species; 90% and 80% for cisco and lake whitefish, respectively. Total otolith radius and otolith radius at each annulus was measured at the posterodorsal area of the otolith. These measures were used to back-calculate fork length of fish at each age. The relation between fork length and total otolith radius was established using the different regression models outlined by Jonsson and Stenseth (1976). The third degree polynomial

was chosen as the mean square deviation between observed and estimated fish lengths was lowest. The relation between total otolith radius and fork length was estimated for both species with the 1979 to 1981 data as there was no difference graphically between the years. The equation of the third degree polynomial relating fork length to total otolith radius for cisco ($n = 894$) is

$$L = 9.68 - 9.45\,X + 130.69\,X^2 - 31.16\,X^3$$
$$r^2 = 0.989,$$

where L is fork length in millimetres and X total otolith radius in millimetres. For lake whitefish ($n = 903$) the corresponding equation is

$$L = -59.25 + 135.11\,X + 87.35\,X^2 - 25.48\,X^3$$
$$r^2 = 0.994.$$

The following correction was applied if total otolith radius of a fish of a given length was different than the average otolith radius for that length (Bagenal 1978):

$$S_n = \frac{S\,s_n}{s},$$

where S_n is the adjusted distance to the nth annulus; S is the average otolith radius for a fish of the observed length; s_n is the radius of the nth annulus; and s is the total otolith radius.

Mean fork length at each age for each sex was estimated with the back-calculated fork length at the last complete annulus to eliminate variance caused by the date of fish capture. Differences among means for each sex between years and for each year between sexes were tested using the t-test for paired comparisons (Sokal and Rohlf 1981). Back-calculated fork lengths at each age for fish of the same cohort sampled in different years were also analysed to detect any possible Lee's phenomenon which might indicate possible bias in growth curves due to size selective mortality or sampling bias (Ricker 1975). Between years comparisons were done by analysis of variance (Sokal and Rohlf 1981). Back-calculated fork lengths at the last complete annulus were fitted to a von Bertalanffy growth model to describe changes in length with age (Ricker 1975). The model was fitted using an iterative, nonlinear regression computer program (SAS 1985, NLIN procedure) described by Vaughan and Kanciruk (1982).

In northern fish populations, individuals do not spawn yearly and there is no simple criterion for identifying age at maturity. There is normally an increase in proportion of maturing fish with age which peaks at an age and level set by the frequency of spawning, the age at first maturity, and the pattern of mortality (Morin et al. 1982). Furthermore, no spawning marks which could indicate the past history of cisco and lake whitefish are observed. For these reasons, the youngest age-group in which at least 50% of the fish were maturing to spawn was adopted as the age at maturity.

Patterns of seasonal growth and CPUE were used to calculate catch curves. Fish were divided in length classes of 20 mm and a length frequency distribution established. Length frequency distributions were corrected to remove the effect of date of capture on length of fish using logistic curves describing seasonal increase in length. A frequency table relating length classes to proportion of fish of the same age in the different length classes was made and used to estimate the CPUE of fish of each age class. The annual survival rate was estimated from the catch curves relating the logarithms of CPUE and age with the data of 1979 to 1981 (Ricker 1975).

Fecundity of the two species was calculated by regressing fecundity on length (log transformed data) and compared by analysis of covariance (Sokal and Rohlf 1981).

Lifetime Reproductive Success

The maximum lifetime fecundity was selected as the measure of success of each species since these populations are believed to be in stable equilibrium with their physical and biotic environment (Morin et al. 1982). The expected lifetime fecundity was measured by

$$(1)\quad F = \sum_{t=x}^{y} l_t m_t,$$

where l_t is the age-specific survival rate, m_t the age-specific fecundity, x the age at sexual maturity and y the age at death. First, a complete schedule of survival and fecundity was made for each female population. The survival rate for juveniles older than three and adults were estimated with the CPUE at age and the catch curves. The survival rate per year between birth and age three was estimated with the relative egg production of the female populations for each year and the mean CPUE at age 3. The relative egg production of the female populations was estimated by:

$$(2)\quad Ep = \sum_{t=x}^{y} \mathrm{CPUE}_t\, R_t\, m_t,$$

where CPUE_t is the catch per unit of effort of fish of age t, R_t the proportion of spawners in age class t, m_t the number of female births at age t and the parameters x and y the minimum and maximum age of spawners observed, respectively. The number of female births at each age was evaluated by:

$$(3)\quad m_t = 10^{(a + b \log (L_\infty (1 - e^{-K(t+1-t_0)})))}/2,$$

where the von Bertalanffy equation gives the length of fish of age t at reproduction (in the equation age $t+1$ since the equation gives the length at the beginning of the season and the fish are spawning in the fall at a length corresponding to an age of $t+1$) and a and b are the coefficients of the regression of the logarithm of fecundity on the logarithm of length. The division by 2 gives the number of female births assuming a ratio of 1/1 between males and females (observed male/female ratio for cisco 1.05/1 and for whitefish 1.16/1). The estimate of survival between birth and age 3 is calculated by dividing the CPUE of age 3 by the obtained value of egg production of the adult population.

The optimal age at maturity for individuals maximizing the expected lifetime fecundity was estimated by setting $l_0 = 1$ (number of fish at age 0) and using the calculated age-specific survival rates. Lifetime fecundity of individuals was estimated for different ages at first reproduction and a 2-yr interval between spawnings as the two species are unable to reproduce in successive years (Morin et al. 1982; Dodson et al. 1985; Lambert and Dodson 1990). Female birth rate was estimated with equation (3) given above.

Results

Life History Traits

Lake whitefish can live up to twice as long as cisco in the Eastmain River (Fig. 1). Most cisco are less than 8 yr old and

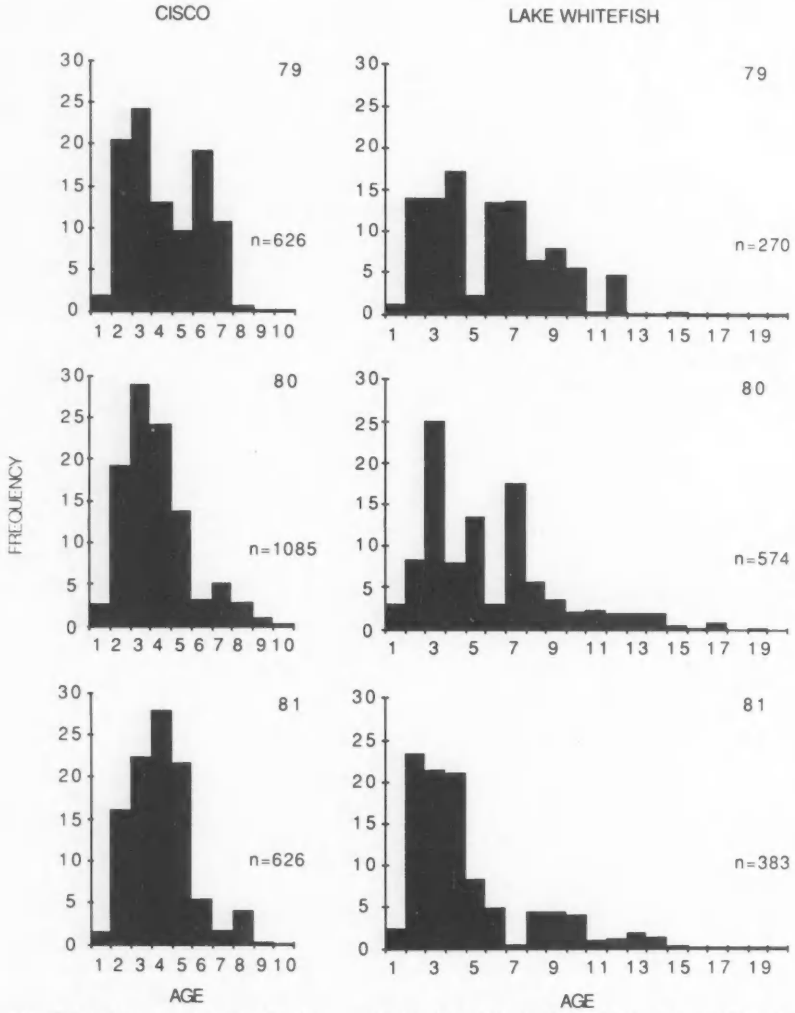

FIG. 1. Age-frequency distribution of cisco and lake whitefish in the Eastmain River from 1979 to 1981.

TABLE 1. Parameter estimates of the von Bertalanffy equation for cisco and lake whitefish of the Eastmain River with the grouped data of 1979 to 1981. L_t is length at year t; L_∞ is the asymptotic length; K is the growth rate; t_o is a constant inserted to improve the fit; and n is the number of fish analysed.

		L_∞	K	t_o	n
Lake whitefish	Male	422.5	0.238	0.016	452
	Female	439.2	0.222	0.001	451
Cisco	Male	328.5	0.331	0.206	430
	Female	344.7	0.324	0.293	464

most lake whitefish are less than 14 yr old. The age frequency distributions also show the low abundance of the 1974 year class (age 5 in 1979) for both species for the 3 yr analysed (Fig. 1).

Comparisons of mean fork lengths back-calculated to the last complete year of growth showed no consistently significant differences for both species (t-test for paired comparisons; for eight tests, $P>0.05$; for four tests, $0.01<P<0.05$) between the years for each sex. Therefore, all other analyses were carried out on the grouped data over 3 yr. Sexes were analysed separately as female growth and mortality rates were required in subsequent analyses.

Comparisons between back-calculated mean fork length at the same age for fish of the same sex and of the same cohort sampled in different years did not differ significantly ($0.01<P<0.05$, but in 90% of the analyses at $P>0.05$). For example, the back-calculated fork length at each age for female cisco of age 5 in 1979, 6 in 1980, and 7 in 1981 did not differ significantly. Thus, there was no evidence for Lee's phenomenon.

Von Bertalanffy growth curves calculated for each sex of both species indicated significant differences ($P<0.001$) in all parameters between the two species and between sexes within each species (Table 1). Asymptotic length was greater for lake whitefish than cisco and greater for females than males of both

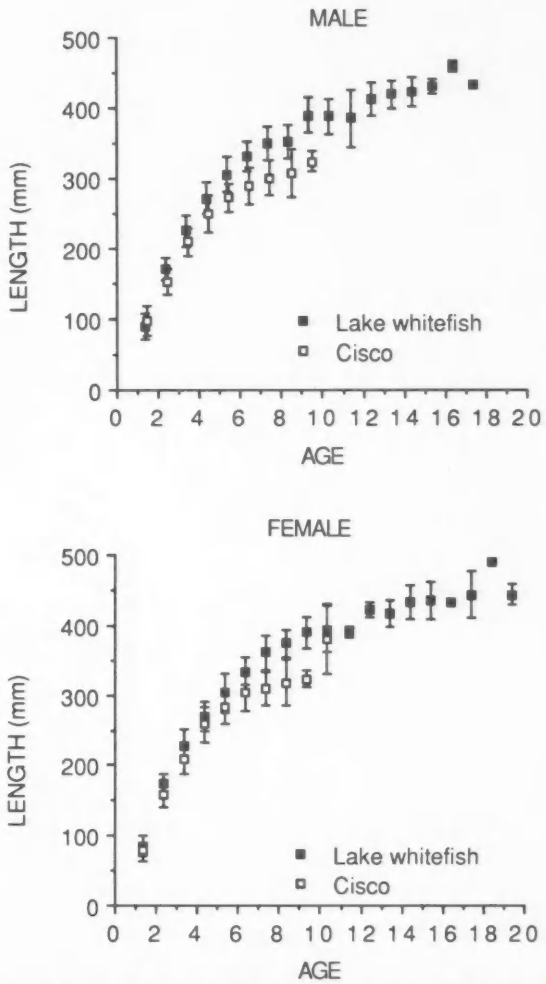

FIG. 2. Mean lengths at age of male and female cisco and lake whitefish for the grouped data of 1979 to 1981. Vertical bars indicate standard deviation.

species. Mean fork lengths at age were greater for lake whitefish and growth rate coefficient (K) was greater for cisco. Comparisons of mean fork lengths at age between the two species gave similar results (Fig. 2). Mean fork lengths at age of male and female cisco were significantly lower (t-test for paired comparisons; $P<0.01$) than those of lake whitefish. Such differences were not significant when comparing juvenile cisco and lake whitefish (age 1 to 4; $P>0.05$). However, mean fork lengths at age were not significantly different ($P>0.05$) between sexes within each species.

The age and length frequency distributions of spawning cisco and lake whitefish were evaluated using only fish caught after mid-July when maturity stage could be determined accurately. Only those fish showing a maturity stage of IV or V (classification of Nikolskii 1963) after mid-July were considered able to spawn in the fall. Cisco mature at a younger age and at a smaller size than lake whitefish and, in both species, males spawn earlier than females (Fig. 3). The age at first reproduction was 4+ for male and 5+ for female cisco and 6+ for male and 7+ for female lake whitefish. In addition, no male and female lake whitefish were mature at the age of 4+ and 5+, respectively while in male and female cisco 60 to 77% of the fish were mature at these ages. In both species, males spawned at a smaller size than females (Fig. 3).

Cisco showed a significantly higher fecundity than lake whitefish (Fig. 4). The slopes of the two regressions did not differ significantly ($F=0.03$, $P>0.75$) but the adjusted mean fecundity was higher for cisco ($F=37.91$, $P<0.001$). Female cisco produced about 40% more eggs than female lake whitefish of the same length. However, considering the age at maturity, a 5-yr-old female cisco produced 34% fewer eggs than a 7-yr-old female lake whitefish.

The analysis of CPUE at age revealed a higher adult mortality rate for cisco than lake whitefish as demonstrated by the steeper slope of the catch curve for cisco (Fig. 5). Since those populations are only lightly exploited, we considered mortality rates as representing natural mortality. Comparisons between the slopes of the regressions lines (Table 2) indicated significant differences ($P<0.05$) between cisco and lake whitefish and no significant difference ($P>0.05$) between sexes within each species. Comparison of mortality rates for juvenile fish (Table 3) calculated with the mean CPUE at age (age 3 to 5; lower ages being incompletely sampled) indicated no significant difference between the two species (t-test; $P>0.05$). As juveniles, cisco and lake whitefish have similar mortality rates but as adults mortality rates are significantly higher in cisco than in lake whitefish (Table 3).

Lifetime Reproductive Potential

The CPUE of each age class for each year, combined with the proportion of spawning females in these age classes (Fig. 3) and their fecundity gave relative estimates of egg production for the two adult female populations. The number of eggs produced each year is $5.6 \cdot 10^4 \pm 1.7 \cdot 10^4$ for cisco and $1.9 \cdot 10^4 \pm 0.8 \cdot 10^4$ for lake whitefish. From these results and the mean estimates of CPUE at age 3 we obtain mean survival rates per year between age 0 and 3 of $5.5 \cdot 10^{-2} \pm 0.6 \cdot 10^{-2}$ for cisco and $4.9 + 10^{-2} \pm 0.6 \cdot 10^{-2}$ for lake whitefish.

With the schedule of survival, fecundity, and the proportion of spawners at each age, $l_x m_x$ is obtained for the female population of each species (Table 4 and 5). $l_x m_x$ at each age shows that the highest contribution in number of offspring for cisco is produced by age class 5 while the contribution is more equally distributed between ages 7 to 9 for lake whitefish with the highest contribution at age 8. The summation of the $l_x m_x$ products at each age indicate that both populations can be considered stable, as the summations give values close to one. The estimated rate of increase of populations numbers (Malthusian parameter r) is close to zero for both populations (0.002 for cisco and 0.026 for lake whitefish). The expected lifetime fecundity (F equation (2)) of individual females was estimated for different ages at maturity using the age-specific survival rates of juveniles and adults (Table 3), the estimates of fecundity and growth parmeters and a 2-yr interval between spawnings. The age at maturity maximizing expected lifetime fecundity corresponds to an age of 4.2 for female cisco which is lower than the observed age at maturity (Table 6). Within the standard errors of estimates for juvenile and adult survival rates and with other variables kept constant, the optimal age at maturity varies between 3 and 5.6 (Table 6). To predict an optimal

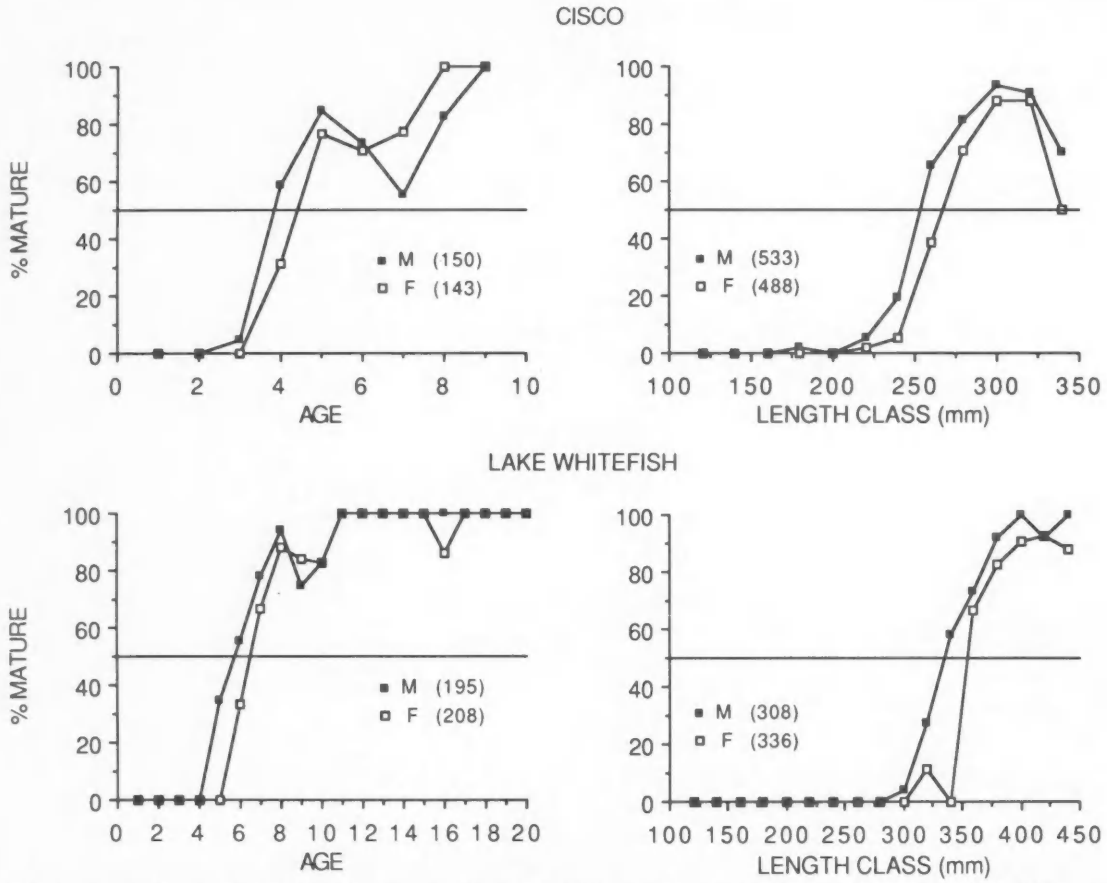

FIG. 3. Percentages of mature male and female cisco and lake whitefish by age and length class. Horizontal line represents the 50% mature level. Numbers in parentheses represent the number of fish.

age at maturity equal to the observed age at maturity of female cisco (5), we must postulate a juvenile survival rate of 0.82 which is within the standard error of the estimate of juvenile survival rate (Table 3). For female lake whitefish, the combination of the mean estimates of the different variables do not result in an age where the expected lifetime fecundity is maximized. This is caused by the similarity between juvenile and adult survival rate. Within the standard errors of the estimates of juvenile and adult survival rates, the optimal age at maturity varies between no minimum value to a maximum value of 6.2 which is lower than the observed age at maturity (Table 6). To predict an optimal age at maturity equal to the observed age at maturity of female lake whitefish (7), we must postulate a juvenile survival rate of 0.89 and an adult survival rate of 0.71 (Table 6). These values are close to the range within the standard errors of the mean estimates of juvenile and adult survival rates (Table 3).

The sensitivity of optimal age at maturity to the estimation errors for different variables was examined for both female populations (Table 7). Age at maturity is very sensitive to changes in juvenile survival rate; an 8–10% change in juvenile survival rate producing changes between 0.8 and 3.4 yr in the optimal age at maturity (Table 7). Age at maturity is also sensitive, but to a lesser degree, to changes in adult survival rate, growth rate (K) and the slope of the regression (b) of the fecundity–length function. However, for similar variations in the optimal age at maturity, lower coefficients of variation are observed for the growth rate parameter. Changes in mean juvenile survival rate between birth and age 3, in asymptotic length (L_∞) and in the parameter t_o of the growth curve had no effect on the optimal age at maturity (Table 7).

The age at first reproduction is important for both species as the contribution in fecundity by the first reproduction represents 67% (age 5) of the lifetime fecundity of cisco and 42% (age 7) of the lifetime fecundity of lake whitefish. The first two reproductive events in lake whitefish represent 68% of the lifetime fecundity. The number of reproductive events to realize the expected lifetime fecundity is also different between the two species; 97% of the lifetime fecundity is achieved in the first three spawnings in cisco whereas in lake whitefish this percentage is attained after the sixth spawning.

Discussion

Cisco and lake whitefish are closely related species and exhibit a wide range of variations and considerable overlap in

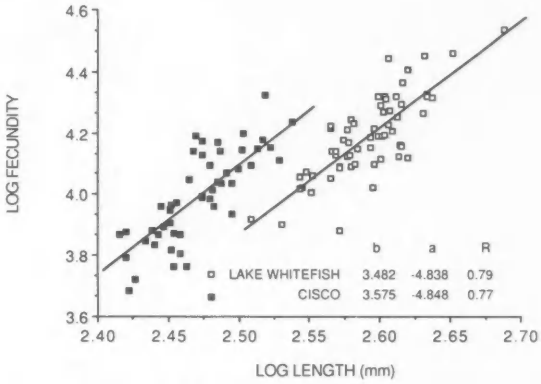

FIG. 4. Regressions of the logarithm of fecundity on the logarithm of length for cisco and lake whitefish sampled from 1979 to 1981. Values *a* and *b* represent the intercept and the slope of the regression equations respectively and *r* the correlation coefficient.

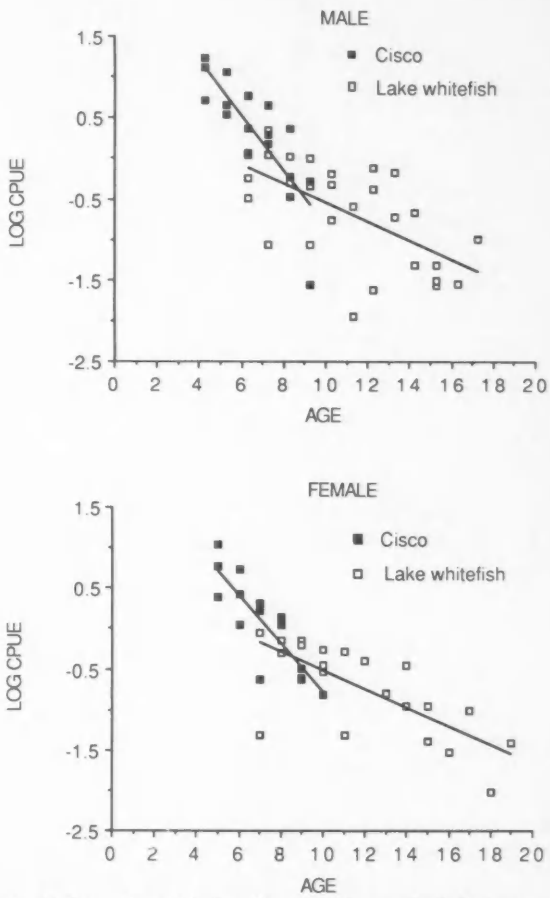

FIG. 5. Regressions of the logarithm of catch per unit of effort on age for male and female adult cisco and lake whitefish for the data of 1979 to 1981.

their life history characteristics (Jensen 1981, 1985; Scott and Crossman 1974). However, in the same environment (Eastmain River) differences in life history characteristics are observed and result in different ages at maturity. Considering the Eastmain populations of cisco and lake whitefish stable, the age at maturity of cisco and lake whitefish corresponds, within the standard error of the estimates of the different life history characteristics, to the age at maturity maximizing their overall lifetime reproductive potential (Table 6). As expected, the lower age at maturity of cisco is associated with a higher growth rate and a higher mortality than lake whitefish. Lake whitefish achieve expected lifetime fecundity (97%) with twice the number of spawnings (because of higher adult survival) than cisco. This may be viewed as a measure of the degree of iteroparity, with lake whitefish being more iteroparous than cisco.

Empirical studies using different approaches demonstrate the relative importance of different life history characteristics in determining the optimal age at maturity. For example, Jensen (1985) estimated that changes in the survival of immature fish and the age at maturity, which was related to length at maturity, growth rate and asymptotic length, were the only parameters that had a large effect on the net reproductive rate of lake whitefish. Jonsson et al. (1984) showed that the age maximizing overall lifetime reproductive potential in cutthroat trout (*Salmo clarki*) and Dolly Varden charr (*Salvelinus malma*) was sensitive to small changes in juvenile mortality rate, individual growth rate, and the malthusian parameter (r) but insensitive to variations in the other parameters. Roff (1984) modeled the important life history parameters determining the age at first reproduction. The analysis of the model with respect to the expected lifetime fecundity showed that age at first reproduction was dependent on natural mortality rate, growth rate (K) and on the regression coefficient of the fecundity–length function which was assumed constant (value of 3) in the model.

From the predictions of these models, the observed combination of life history characteristics and the sensitivity of age at maturity to these different parameters, the difference in age at maturity between cisco and lake whitefish can be attributed to differences in juvenile and adult survival rate and growth rate. The slopes of the regressions of the fecundity–length functions are not important in explaining the different age at maturity between the two species since no significant differences ($P>0.75$) in the slopes of the regressions were observed.

Juvenile Survival

Several studies have shown the influence of juvenile survival on life history patterns. For example, Stearns and Crandall (1981) obtained a correlation of 0.929 between predicted and observed age at maturity for nine populations of lizards and salamanders with a model based on the survival of juveniles. Glebe and Leggett (1981) concluded that predictability of the reproductive environment, through its influence on juvenile mortality, was the principal regulator of latitudinal differences in life history strategies in shad. Bell (1980), using models based on reproductive costs in time-varying environments, reached similar conclusions about the effect of juvenile survival. No significant differences in juvenile survival rates were observed between cisco and lake whitefish for either juveniles between age 0 and 3 or juveniles in prereproductive years (between 3 and age at maturity).

TABLE 2. Regressions of the logarithm of catch per unit of effort (Y) on age (X) for adult cisco and lake whitefish of each sex for the data of 1979 to 1981. F = F-value for the significance of the regression; P = probability level of significance; r = correlation coefficient; and n = number of observations. The instantaneous rate of mortality is obtained by changing the sign of the regression slope, and multiplying by 2.3026.

Species	Sex	Regression equation	F	P	r	n
Cisco	Male	$Y = 2.370 - 0.334\,X$	31.7	<0.001	0.82	17
	Female	$Y = 2.197 - 0.298\,X$	29.5	<0.001	0.84	14
Lake whitefish	Male	$Y = 0.520 - 0.117\,X$	16.8	<0.001	0.62	29
	Female	$Y = 0.638 - 0.115\,X$	24.6	<0.001	0.73	23

TABLE 3. Instantaneous rate of mortality (Z) with standard deviation (SD) and corresponding survival rate (S) for juvenile and adult cisco and lake whitefish. Standard deviation estimated from the mean CPUE at age for juveniles and from regression equations for adults.

	Z	SD	S	± SD
Cisco				
Juvenile (age 3 to age at maturity)	0.234	0.084	0.792	0.728–0.860
Adult Male	0.769	0.136	0.463	0.405–0.531
Female	0.686	0.127	0.503	0.444–0.572
Lake whitefish				
Juvenile (age 3 to age at maturity)	0.271	0.151	0.763	0.656–0.887
Adult Male	0.269	0.067	0.764	0.715–0.817
Female	0.265	0.053	0.767	0.728–0.809

TABLE 4. Schedule of survival and fecundity for the female population of cisco and the contribution to female births of each age class with $l_o = 1$. l_t is the probability of surviving from birth to age t; R is the proportion of spawners in age class t; m_t is the number of female births at age t; and $l_t m_t$ (R) is the contribution of each age class to female births in the population.

Age	l_t	R	m_t	$l_t m_t(R)$
0	1.0	0.0		
1	$5.5 \cdot 10^{-2}$	0.0		
2	$3.1 \cdot 10^{-3}$	0.0		
3	$1.7 \cdot 10^{-4}$	0.0		
4	$1.3 \cdot 10^{-4}$	0.315	3479	0.146
5	$1.1 \cdot 10^{-4}$	0.765	4536	0.367
6	$5.3 \cdot 10^{-5}$	0.705	5432	0.204
7	$2.7 \cdot 10^{-5}$	0.775	6155	0.128
8	$1.4 \cdot 10^{-5}$	1.0	6719	0.091
9	$6.8 \cdot 10^{-6}$	1.0	7149	0.049
10	$3.4 \cdot 10^{-6}$	1.0	7473	0.026
11	$1.7 \cdot 10^{-6}$	1.0	7714	0.013
12	$8.7 \cdot 10^{-7}$	1.0	7891	0.007
				$\Sigma l_t m_t = 1.030$

TABLE 5. Schedule of survival and fecundity for the female population of lake whitefish and the contribution to female births of each age class with $l_0 = 1$. l_t is the probability of surviving from birth to age t; R is the proportion of spawners in age class t; m_t is the number of female births at age t; and $l_t m_t$ (R) is the contribution of each age class to female births in the population.

Age	l_t	R	m_t	$l_t m_t(R)$
0	1.0	0.0		
1	$4.9 \cdot 10^{-2}$	0.0		
2	$2.5 \cdot 10^{-3}$	0.0		
3	$1.2 \cdot 10^{-4}$	0.0		
4	$9.3 \cdot 10^{-5}$	0.0		
5	$7.1 \cdot 10^{-5}$	0.0		
6	$5.4 \cdot 10^{-5}$	0.330	5064	0.090
7	$4.1 \cdot 10^{-5}$	0.665	6067	0.166
8	$3.2 \cdot 10^{-5}$	0.880	6967	0.194
9	$2.4 \cdot 10^{-5}$	0.840	7754	0.158
10	$1.9 \cdot 10^{-5}$	0.830	8427	0.130
11	$1.4 \cdot 10^{-5}$	1.0	8996	0.128
12	$1.1 \cdot 10^{-5}$	1.0	9470	0.104
13	$8.4 \cdot 10^{-6}$	1.0	9863	0.083
14	$6.5 \cdot 10^{-6}$	1.0	10185	0.066
15	$5.0 \cdot 10^{-6}$	1.0	10449	0.052
16	$3.8 \cdot 10^{-6}$	1.0	10663	0.041
17	$2.9 \cdot 10^{-6}$	1.0	10837	0.032
18	$2.2 \cdot 10^{-6}$	1.0	10978	0.025
19	$1.7 \cdot 10^{-6}$	1.0	11092	0.019
20	$1.3 \cdot 10^{-6}$	1.0	11184	0.015
21	$7.8 \cdot 10^{-7}$	1.0	11257	0.011
				$\Sigma l_t m_t = 1.313$

Variations in mean juvenile survival rate between age 0 and 3 (mostly the result of low egg and larval survival) have no effects on the age at maturity of both species (Table 7). Thus possible differences and year-to-year fluctuations in juvenile survival rates between age 0 and 3 will not affect the observed age at maturity unless mean juvenile survival rate changes in the long term, in which case the two populations would no longer be stable. In such a case, the malthusian parameter r would be a more suitable measure of fitness than the expected lifetime fecundity. If r is the parameter maximized, the mean juvenile survival between age 0 and 3 (egg and larval survival) could then influence the age at maturity as demonstrated by the model of Roff (1984).

Juvenile survival rate in preproductive years (between 3 and age at maturity) has the largest influence on the optimal age at maturity; an 8–10% change producing changes from 0.8 to 3.4 yr in the optimal age at maturity (Table 7). Thus, the observed age at maturity of cisco and lake whitefish should be strongly influenced by juvenile survival rate in prereproductive years. However, differences in the age at maturity between cisco and lake whitefish cannot be attributed solely to differences in juvenile survival rate. The different juvenile survival rates (between 3 and age at maturity) of cisco and lake whitefish, although not statistically different (Table 3), contribute to the different ages at maturity of the two species. Based on the estimates of juvenile survival rates predicting the observed age at maturity of both species (Table 6), we observed that an increase in juvenile survival rate for cisco to a value equal to the predicted value

TABLE 6. Age at maturity maximizing the expected lifetime fecundity for the combination of the mean estimates of the life history parameters, minimum and maximum age at maturity within the standard deviations of juvenile older than 3 yr (S1) and adult (S2) survival estimates and juvenile and adult survival rate needed to predict an optimal age at maturity equal to the observed age at maturity.

	Survival rate	Optimal age at maturity
Cisco		
Mean estimates of parameters	S1 = 0.792 S2 = 0.503	4.2
Minimum within SD of survival rates	S1 = 0.860 S2 = 0.572	3.0
Maximum within SD of survival rates	S1 = 0.728 S2 = 0.444	5.6
Estimates of survival rates predicting the observed age	S1 = 0.844 S2 = 0.503	5.0
Lake whitefish		
Mean estimates of parameters	S1 = 0.763 S2 = 0.767	0
Minimum within SD of survival rates	S1 = 0.656 S2 = 0.809	0
Maximum within SD of survival rates	S1 = 0.889 S2 = 0.728	6.2
Estimates of survival rates predicting the observed age	S1 = 0.895 S2 = 0.705	7.0

for lake whitefish increased the optimal age at maturity for cisco by almost 1 yr (age 6). This change shows the importance of variations in juvenile survival rate on the age at maturity but also demonstrates that the difference in juvenile survival rate (between 3 and age at maturity) between cisco and lake whitefish is not a sufficient factor to explain their different age at maturity.

Growth Parameters

Variations in growth rate also explain the difference in age at maturity of cisco and lake whitefish. For example, decreasing cisco's growth rate to a value of 0.2223 (observed K for lake whitefish) without changing fecundity and mortality increases optimal age at maturity by 1 yr.

As reported by the different studies reviewed by Roff (1984), growth has been related to physiological processes and environmental factors such as temperature and food and to different life history attributes. In the Eastmain River, cisco and lake whitefish (taxonomically close species) are present in the same temperature conditions and are opportunistic feeders, although showing different preference in their prey as adults (Lambert and Dodson 1982b). Cisco generally attain smaller maximum length than lake whitefish but can reach similar size. In Lake Ontario, cisco measure 41.4 cm at the age of 9 and a specimen of 57.2 cm has been captured in Great Slave Lake (Scott and Crossman 1974). The two species as juveniles have equal lengths, the growth curves only beginning to diverge when cisco reach maturity (Fig. 2). This suggests that the different population growth patterns of cisco and lake whitefish is principally associated with the cost of reproduction through its effect on growth and mortality. As both species are able to attain a comparable size, we conclude that differences in the cost of reproduction are responsible for the different population growth rates observed for the two species.

Adult Survival

The results presented for lake whitefish by Jensen (1985) indicate that an increase in mortality is associated with an increased growth rate and an earlier age and smaller size at maturity. A smaller size at maturity and lower growth after maturity results in a lower asymptotic size. In the present study lake whitefish reach a greater maximum age, a greater size, and a later age at maturity whereas cisco exhibit a greater growth rate and a higher fecundity. Morin et al. (1982) observed similar differences in the life history characteristics of the two species in La Grande River located 200 km to the north. Associated with the combination of these life history parameters, different mortality rates are observed in the Eastmain River. As juveniles, cisco and lake whitefish have the same mortality rate but as adults the mortality rate of cisco is significantly higher than that of lake whitefish.

Models of trade-off in energy allocation are based on the assumption that costs in survival are associated with reproduc-

TABLE 7. Sensitivity for estimation errors of the optimal age at maturity. In all estimations, one value is varied and the others are set equal to the population means except for juvenile (age 3 to age at maturity) and adult survival where mean values were replaced by the values predicting the observed age at maturity. For each value, the coefficient of variation (CV) for the estimate and the corresponding change in the optimal age at maturity are presented.

	Cisco		Lake whitefish	
Parameter	CV(%)	Change in the optimal age	CV(%)	Change in the optimal age
Juvenile survival (age 0 to 3)	10	—	13	—
Juvenile survival (age 3 to age at maturity)	8	0.8–1.2	10	2.6–3.4
Adult survival	13	0.2	5	0.2
Asymptotic length	2	—	1	—
Growth rate	6	0.2	3	0.2
Constant (t_o)	23	—	54	—
Fecundity (Regression slope-b)	12	0.2	10	0.2

tion. Apart from the study of Snell and King (1977) on rotifers, few studies give evidence of a direct connection between reproduction and survival probability. Nevertheless, evidence from bioenergetic studies supports the hypothesis. Glebe and Leggett (1981) for example, found a positive correlation between the energy expenditure by shad during freshwater migration and semelparity or iteroparity in these populations. Comparison of reproductive and nonreproductive cisco and lake whitefish indicate that reproduction results in somatic cost to both species but that cisco's higher reproductive effort results in a greater somatic cost in cisco than in lake whitefish (Lambert and Dodson 1990). A higher adult mortality rate for cisco is associated with this higher somatic cost (Table 3).

Using data on different anadromous species and populations, Glebe and Leggett (1981) noted differences in energy loss during freshwater migration associated with semelparity and iteroparity. Iteroparous species consumed less than 60% of their total energy reserves during migration. Semelparous species exhibited energy expenditures associated with migration that exceeded 70% of the total energy available. For example, St-Johns River shad consume 70–80% of their total energy reserves and all shad die following spawning. The 70% value may represent the minimum energy level below which no survival is possible. Cisco and lake whitefish are both iteroparous and, in both species, less than 60% (58% for female cisco and 35–44% for lake whitefish) of their energy reserves are consumed during migration and spawning (Lambert and Dodson 1989). However, if the cost of overwintering is included, cisco and lake whitefish consumed 61–67% of their energy reserves which approach expenditures typical of semelparous species. Assuming comparable energy expenditures for reproductive and nonreproductive fish during winter, reproductive female cisco would theoretically consume ≈84% of their energy reserves for migration, reproduction and overwintering compared with the observed value of 67%. Thus, we may hypothesize that cisco consuming more than approximately 67% of their energy reserves would not survive. The difference in mortality between cisco and lake whitefish may result from the different proportions of fish of each species that utilized more than a critical percentage of their energy reserves for migration, reproduction, and overwintering.

The higher somatic cost of reproduction in cisco will result in a greater proportion of cisco with an energy level close to the minimum level necessary to survive. Compared with lake whitefish, a higher proportion of cisco will experience energy expenditures greater than the critical limit. It is also reasonable to assume that annual mortality rate in reproductive cisco will be more likely to vary with fluctuations in environmental conditions. A small decrease in the accumulation of energy during the summer may, for example, increase the proportion of reproductive cisco that will exceed the minimum energy threshold. The lower proportion of lake whitefish near the minimum energy threshold may result in lower variations in the mortality rate of reproductive lake whitefish due to fluctuations in environmental conditions.

When fecundity increases with size, present reproduction involves an additional risk of failing to realize a greater future fecundity (fecundity cost) if reproduction increases mortality (Bell 1980). The somatic cost of reproduction also results in fecundity cost for both cisco and lake whitefish. Reproduction reduces future fecundity potential for the two species because the reduced energy level of reproductive fish after migration, reproduction, and overwintering obliges fish to miss the next spawning season (Lambert and Dodson 1990), increasing the risk of mortality before the next reproduction. The fecundity cost will also be higher in cisco than in lake whitefish since reproduction results in a higher mortality in cisco.

The energy cost of migration is largely responsible for the higher somatic cost of reproduction in cisco compared with lake whitefish (Lambert and Dodson 1990). Consequently, the cost of migration contributes significantly to the observed species-specific adult mortality patterns.

Differences in the distance and difficulty of migration in the river systems of James and Hudson Bay may explain why intraspecific comparisons of life history traits of anadromous cisco and lake whitefish along the James and Hudson Bay coast do not clearly conform to the theory that predicts reduced fecundity, increased age at maturity, and more iteroparity northwards (Morin et al. 1982). Climatic data summarized by Morin et al. (1982) shows that climatic conditions are harsher at northern sites of Hudson Bay. We hypothesize that the differences in difficulty and distance of migration along the James and Hudson Bay coast can explain differences between observed and expected patterns of reproductive traits for cisco and lake whitefish. In the Eastmain river, migration extends 33 km, in which 7 km are rapids. For more northerly rivers, migration distance ranges from 13 km in the southern part of Hudson Bay to 3 km near the northern limit of distribution. There are no rapids before the spawning grounds in these rivers (Morin et al. 1980). Consequently, there is a decrease in the cost of migration with latitude and a decrease in the energy available because of shorter growing seasons with latitude. We propose that the observed reproductive traits may not be different from those expected theoretically if the cost of migration is included in the somatic cost of reproduction. For example, cisco exhibit delayed maturity and reduced growth in the north of James Bay and Hudson Bay (Morin et al. 1982). This implies that adult survival must increase or at least remain unchanged. As fecundity remains unchanged over the same range, comparable or improved adult survival can only be related to comparable or lower somatic costs of reproduction afforded by lower migration costs. However, in the absence of data on resource input, costs of migration and costs of reproduction for the observed fecundities, the adaptive significance of the age at maturity and fecundity observed over large latitudinal gradients cannot be interpreted in the context of life history theory.

Acknowledgments

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Sea Surface Temperatures along the Coast of British Columbia: Regional Evidence for a Warming Trend

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Sea-surface temperature has been measured at a large number of sites around the coast of British Columbia for periods well in excess of 50 yr. These time series are long enough to give clear evidence of a large scale secular warming. For the purposes of this paper the daily SST observations are decimated to monthly mean values. The observations are of particular value because observation methods have remained invariant throughout the observation period, and many of the stations are remote from civilisation allowing trends to be estimated that have not been contaminated with urbanization effects. Eighteen out of nineteen stations that are currently being sampled show a warming trend, the one that shows a cooling trend is the shortest time series, only in its eleventh year. The sea-surface temperatures at sites exposed to the Pacific Ocean show very high coherence with global scale air temperature variations but no relationship to the El Niño/Southern Oscillation signal.

Le long des côtes de la Colombie-Britannique, on a mesuré la température de la surface de l'eau à un grand nombre de sites pendant des périodes dépassant nettement 50 ans. Ces séries chronologiques sont assez longues pour révéler clairement un réchauffement séculaire à grande échelle. Pour les besoins de notre étude, les mesures quotidiennes de la température ont été ramenées à des valeurs mensuelles moyennes. Les mesures sont d'un intérêt particulier du fait que les méthodes employées n'ont pas varié pendant toute la période d'observation, et que bon nombre des stations se trouvent éloignées des zones peuplées, de sorte que les tendances relevées n'ont pas été affectées par l'urbanisation. Dix-huit des dix-neuf stations actuellement en service montrent une tendance au réchauffement, alors que celle qui révèle un refroidissement a donné la série chronologique la plus courte, puisqu'elle n'en est qu'à sa onzième année. Les températures de la surface de la mer relevées aux sites exposés à l'océan Pacifique montrent une très forte concordance avec les variations de la température de l'air à l'échelle du globe, mais aucune relation avec le signal de l'ENSO.

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In recent years considerable effort has been invested in the analysis of temperature observations from around the world and the description of the global or hemispheric variations in atmospheric temperature. Examples are: Jones et al. (1986a, b); Jones (1988); and Hansen and Lebedeff (1987). It is clear from these reports (particularly that of Hansen and Lebedeff 1987) that large scale variations in temperature have occurred over the past 150 yr, with time scales of a few decades, that large scale secular trends exist in global or hemispheric atmospheric temperature as represented by these constructions of temperature chronologies. Over smaller spatial scales the results are somewhat less clear. Hanson et al. (1989) failed to observe any significant trend in climatic records over the United States contiguous states. Regional variations in trend statistics are not surprising, but could have enormous local significance especially if extrapolated into the future. It is believed, for example, that low frequency changes in the climatic state of the ocean off the coast of British Columbia can significantly alter the migration paths of salmon, (Mysak 1986), and there is a genuine concern among local fisheries managers that a permanent change in the climate could produce permanent changes in the distribution and behaviour of commercially important species.

Over the ocean such investigations are severely limited by a lack of data; there are very few locations where sea-surface temperature (or any other ocean climate indicator) has been measured for periods comparable with the atmospheric variables. Nevertheless there is convincing evidence that the climatic state of the ocean does change very substantially. Roemmich and Wunsch (1984) reported on a comparison of two sections in the north Atlantic (the first being a bottle survey and the second a conductivity–temperature–depth (CTD) survey) carried out 24 yr apart and showing dramatic changes in the large-scale characteristics of the Atlantic Ocean.

The purpose of this paper is to examine daily sea-surface temperature measurements made over a period of almost 80 yr at shore stations around the coast of British Columbia, Canada, and to compare these observations with the large scale atmospheric temperature signal reported by Jones et al. (1986a) and Jones (1988).

British Columbia Shore Stations

For many years daily sea-surface temperature measurements have been made at various sites around the coast of British Columbia (Fig. 1). Most of the stations are lighthouses, and the measurements have been carried out since the inception of the program (by the Fisheries Research Board of Canada) without

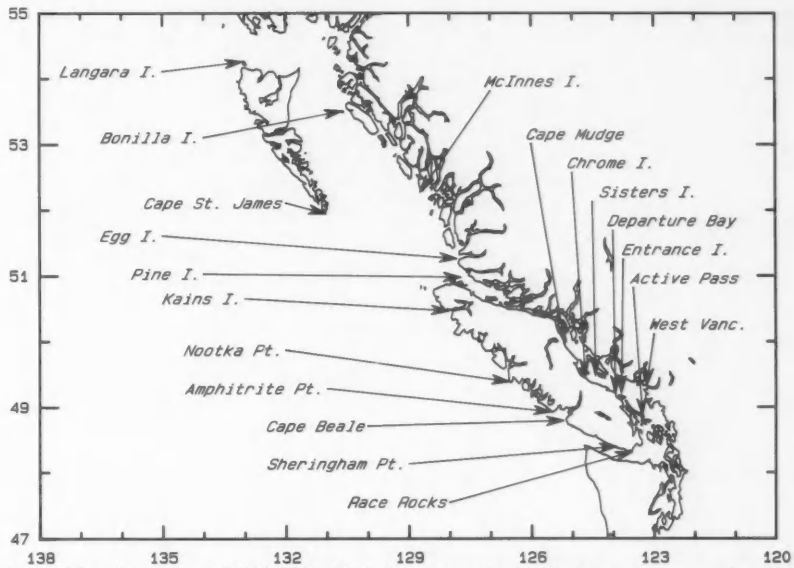

FIG. 1. Map of the coast of British Columbia indicating the sites of the shorestations presently active.

change in instrumentation or procedure. Furthermore, many of the stations are remote from civilization. Thus these observations escape the criticism of Oort et al. (1987) that the establishment of long temperature chronologies "has become almost intractable because of changes in instruments, methods of observations... relocation of land stations, and urbanization effects." The oldest station still operating is Departure Bay which began operation in 1915. The second station to begin operation was Race Rocks, to the south of Victoria, in the Juan de Fuca Strait, which began in 1921. Following those two early stations, a large group (nine stations) began operation in 1934–37, and a few stations started in the late 1960s and 70s. All of the stations that will be discussed in this paper are still reporting data in 1989 except for one. Cape Mudge (in the Strait of Georgia) began operation in 1937 and ceased in 1985, this is included because it ran until very recently and provided very high quality data. Data quality is a subjective matter: here we report an objective measure that is based on the number of times the lighthouse keeper failed to take a measurement, or on the number of times we have had reason to be critical of procedure and so have discarded data.

In all cases but one the location of the temperature observations has varied by only a few metres throughout the history of the observing site. However, between June 1940 and May 1941 a site at William Head (southwest of Victoria, B.C.) was moved to Race Rocks (about 1.8 km away). The data analysed here use these two stations (William Head/Race Rocks) merged into a single composite series which we will call Race Rocks. The observations at Nootka Point are included here, for completeness, but deserve some special mention. The time-series was initiated in 1934, and so rates as one of the older stations, but was terminated in 1953. Then, in response to a need to support a burgeoning local fish-farm industry the observations were resumed in 1987. Hence, the time-series, though starting early and continuing at the present time, is dominated by a single large gap and so contains a relatively small quantity of information. In the interests of objectivity this station is included, but statistics must be read with caution.

A summary of the shore station data up to 1970 is available in Hollister and Sandnes (1972). This useful report also describes the instructions given to the observers and includes photographs of the observing sites. Some of the shore station observers record sea-surface salinity: these observations are also included in Hollister and Sandnes' report, but will not be discussed here as the data appear to be of uncertain quality and were not acquired with a constant procedure.

For the purposes of this paper the daily sea-surface temperature data are decimated by computing monthly mean values. The monthly mean SSTs are then converted to anomalies by computing the SST averaged over all Januarys, Februarys etc, to define an average annual cycle for that station, and subtracting that cycle from the monthly mean SSTs. In the rest of this paper we will always be referring to the anomaly of sea-surface temperature.

Sea Surface Temperature Statistics

In order to estimate the confidence intervals on various temperature statistics (Table 1) we need to estimate the time required to accumulate one degree of freedom, or one independent observation. According to Lumley and Panofsky (1964) this time is given by the integral time scale of the autocorrelation function, J:

$$J = \int_0^\infty C(t')\, dt',$$

where $C(t') = \overline{T(t+t')T(t)}$ and the average is assumed to be taken over time, t. In practice the autocorrelation function decays rapidly and remains close to zero but significantly positive or negative for long sequences of lags: this makes the estimation of J rather uncertain even when the autocorrelation function behaves very well for short lags. Essentially, any estimate of J will include contributions from a large number of small

TABLE 1. Statistics related to the observations of sea-surface temperature at the British Columbia shorestations. 'Years' indicates the period over which observations have been taken; 'N' the number of distinct monthly mean temperatures computed; 'dof' is the number of degrees of freedom; and '% complete' indicates the ratio of number of observations actually acquired to the number expected. In the final column is the trend in SST with 95% confidence limits indicated.

Site name	Years	N	dof	% complete	Trend ± 95% °C/century
Active Pass	1967–89	268	87	100	6.49 ± 2.20
Amphitrite Point	1934–89	649	214	98.5	0.87 ± 0.68
Bonilla Island	1960–89	318	104	90.9	1.50 ± 1.72
Cape Beale	1978–89	133	42	99.3	2.69 ± 6.91
Cape Mudge	1937–85	571	188	98.4	0.20 ± 0.72
Chrome Island	1961–89	339	111	100	3.09 ± 1.74
Cape St. James	1934–89	578	191	87.8	0.73 ± 0.71
Departure Bay	1915–89	817	270	91.5	0.53 ± 0.48
Egg Island	1970–89	232	75	100	5.27 ± 2.60
Entrance Island	1936–89	636	210	99.8	0.28 ± 0.67
Kains Island	1935–89	652	215	99.7	0.19 ± 0.67
Langara Island	1936–89	595	196	94.1	0.53 ± 0.78
McInnes Island	1954–89	419	138	100	1.40 ± 1.16
Nootka Point	1934–89	248	81	37.7	0.24 ± 1.16
Pine Island	1937–89	627	207	99.5	0.64 ± 0.55
Race Rocks	1921–89	809	268	98.4	0.19 ± 0.32
Sheringham Point	1968–89	254	83	100	5.06 ± 1.99
Sisters Island	1968–89	254	83	100	4.68 ± 2.17
West Vancouver	1979–89	111	35	98.2	−1.99 ± 8.78

positive and negative correlations. The cumulant, J, then diverges like an unconstrained random walk. We escape this problem in the following way: it is well known that a first order Markov process has an exponential correlation function; thus, if monthly observations of temperature T_i, $i = 1, 2, 3$ etc, behave like:

$$T_{i+1} = mT_i + (1-m)r_i,$$

where r_i is a random variable then it is easily shown that:

$$\overline{T^2}C_n = \overline{T_i T_{i+n}} = m^n \overline{T_i^2} = \overline{T_i^2} \exp(-n/N_0),$$

where C_n is the correlation function with lag n months and $N_0 = -1/\ln(m)$. To determine the integral time scale of the actual temperature time series, the decay scale N_0 was estimated by fitting an exponential decay model to the first five observed correlations (after the origin) for each time series. The value of J for that time series was then computed as $J = \int_0^\infty \exp(-n/N_0)dn = N_0$. The resulting values of J varied from a high of about 5 mo to a low value of 2.1 mo, a weighted-mean value, weighted by the amount of data used to estimate J, over all time series was calculated as 3.0 mo and was used to estimate the number of degrees of freedom in each time series listed in Table 1. The estimates computed are not sensitive to the number of correlation values fitted, within reason. The conclusions of this paper remain unchanged whether 2, 5, or 10 points are used in the fit.

Examination of Table 1 indicates that the trend is positive at all stations but one, West Vancouver. For this station the time series is extremely short and the observed negative trend is only about 25% of the 95% confidence interval. In short, that observation is not even remotely significant. Weighted by the amount of data in each series we calculate an average trend of 1.2°C/century ± 1.13. It is clear in Table 1 that some of the individual trends relating to the longer time series are marginally significant at the 95% confidence level, and this is reflected in the average trend and the average 95% confidence level quoted above which also indicates marginal significance.

A comparison of the entries in Table 1 with the station locations of Fig. 1 indicates that a spatial variation in the trend of SST may also be present with somewhat smaller trends in the inside waters of the Strait of Georgia and Juan de Fuca Strait. To look for both a common temporal variation and a possible spatial variation in the low frequency climatic variations, empirical orthogonal functions were calculated. Eight stations were used for this calculation: Amphitrite Point, Kains Island, Cape St. James, Langara Island, Pine Island, Cape Mudge, Departure Bay, and Race Rocks. The first four represent 'outside stations' (i.e. stations exposed directly to the Pacific Ocean) and the last three represent 'inside stations' (i.e. not exposed to the Pacific, but influenced by freshwater runoff). The Pine Island site lies about half way between these two classes. These stations were chosen because their data are all of good quality and extend over at least 50 yr with only small data gaps. The (8×8) covariance matrix was computed and the eigenvalues and eigenvectors examined. The first mode accounts for 66% of the variance in the system, and there seems little point, therefore, in examining the seven higher modes. Using the same order of stations listed earlier, the values associated with the first eigenvector are (0.42, 0.42, 0.36, 0.40, 0.32, 0.30, 0.32, 0.24). Thus this mode represents a 'breathing mode' with in-phase variation of a single process at all stations and with amplitudes somewhat greater at the outside stations. The time series associated with the first eigenvector contains most, but not all, of the trend and is 0.99°C/century ± 0.52 and so is clearly significant at the 95% confidence level. The trend can be evaluated for each individual station by multiplying the trend associated with the first EOF (0.99°C/century) by the amplitude of that mode at each site, 0.42 at Amphitrite Point, for example. Thus we find typical temperature trends of 0.4°C/century and 0.3°C/century at the outside and inside stations, respectively.

Comparison of N.E. Pacific SSTs with Global Processes

Surface air temperature variations from 1851 to 1988 have been compiled and published by Jones et al. (1986a) and Jones (1988). Using these estimates of the monthly air temperature anomalies, averaged over the entire northern hemisphere and with the annual cycle removed, Fig. 2 was plotted. The solid line shows the variation in air temperature, and the shaded area the range of sea-surface temperatures observed off the west coast of British Columbia. (For each month the area shaded lies between the minimum and maximum temperatures observed among Amphitrite Point, Kains Island, Cape St. James, Langara Island and Pine Island. The time-series of air and sea-surface temperatures (Fig. 2) have been filtered with a 12-mo running mean filter to eliminate oscillations with periods less than 1 yr, though the sampling interval of 1 mo was maintained. For the sea-surface temperature series the standard deviation ranges between 0.40 and 0.45°C, and for the air temperatures it is 0.202°C, so the air temperature series has been multiplied by 2.25 to bring the air and water temperatures to a common standard deviation. Clearly, though the amplitudes of variation are different, sea-surface temperature off the west coast of British Columbia and northern hemisphere air temperature share the same time history. Close examination shows that fluctuations in the range of periods from a couple of years to 5 yr are common to both data sources but a lower frequency variability

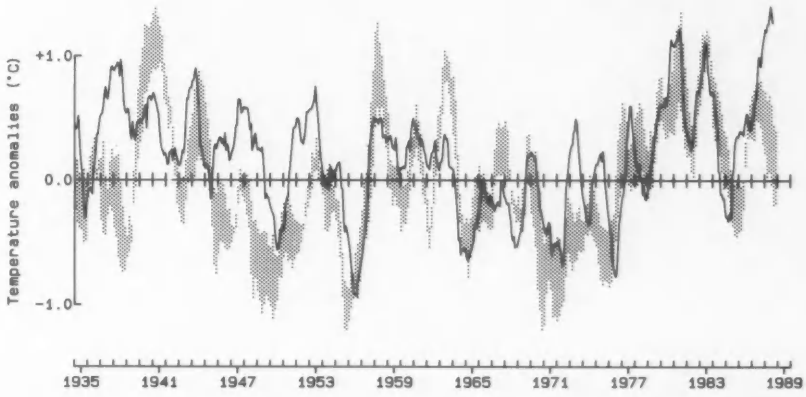

FIG. 2. Anomaly of air temperature averaged over the entire northern hemisphere (solid line, from Jones et al. (1986a, 1988) and the range of sea-surface temperatures observed off the west coast of British Columbia (shaded area). The air temperatures have been normalised to have the same standard deviation as the sea-surface temperatures. For both the air and sea-surface temperatures the annual cycle was removed after computation of the monthly means.

appears not to be in common leading to a separation and return of the two data sets with periods in the 10–20 yr range. Figure 3 shows the coherence between northern hemisphere air temperature and SST averaged over the above five 'outside' stations. For the purposes of the coherence calculations the raw monthly mean anomalies were used, i.e. no filtering was done beyond the calculation of the monthly means and the subtraction of the annual cycle. As expected the coherence is very low at high frequencies (1 cycle/yr); however, coherence is extremely high with essentially zero phase lag over a range of periods extending from 1.5 yr to about 5 yr. A drop in coherence well below the 90% confidence level at very long periods (greater than 10 yr) is also evident. Comparison of the sea-surface temperatures or the northern hemisphere air temperatures with the Southern Oscillation Index (a commonly used diagnostic of El Niño activity) shows no significant coherence.

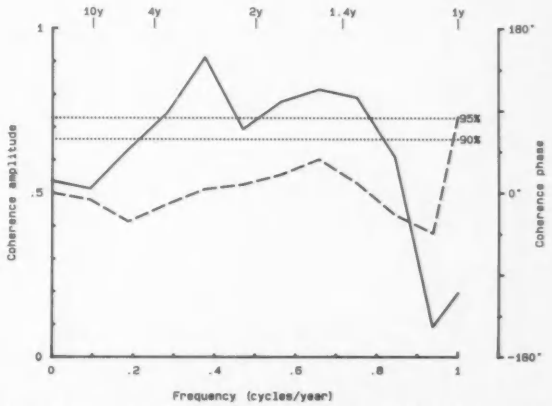

FIG. 3. Coherence amplitude (solid line) and phase (dashed line) plotted against frequency between the anomaly of air temperature averaged over the northern hemisphere and sea-surface temperature anomaly averaged over five "outside" stations, see text. The dotted lines indicate the 90 and 95% confidence levels. The marks above the plot indicate a few periods for ease of reference.

Conclusions

The sea-surface temperature variability observed off the west coast of Canada shows fluctuations that bear a remarkable similarity to the hemispheric variations in air temperature. It is tempting to postulate a cause and effect relationship but we have no convincing relationship to offer. El Niño certainly is a global climatic fluctuation that has particularly clear signature in the eastern Pacific Ocean, but El Niño has periods rather longer than the period of the coherence peak we identify here, and neither SSTs nor the northern hemisphere averaged air temperatures show any coherence with the El Niño signal. This is surprising, because it is clear that most large El Niño events do produce a response in SST off the coast of British Columbia. A notable exception to this rule is the 1972–73 event which was rated in the strong to very strong El Niño category by Quinn and Neal (1987). There are two hypotheses extant that attempt to explain the onset of warm events at high latitudes in response to El Niño events on the equator. The first involves the transformation of the equatorial Kelvin wave that brings the warming event to the coast of Peru into northbound and southbound coastal Kelvin, or coastally trapped, waves. This implies a very direct connection, was first suggested by Clarke (1983) and being direct should produce a high correlation between the southern oscillation index and high latitude SST. The second idea involves the generation of atmospheric pressure anomalies which subsequently drive a response in the high latitude coastal ocean, the so-called atmospheric teleconnection. This concept allowed Emery and Hamilton (1985) to relate SST variations in the high-latitude North Pacific to an index of variation of the northeast Pacific atmospheric pressure field. Thus the variations in SST may be related to the occurrence of El Niño events, but the relationship may be 'second hand' leading to the relatively low correlations and coherences actually computed.

The SST data show trends that are marginally significant at the 95% confidence level and may be showing the first clear evidence of a secular warming trend in the Pacific Ocean. The consequences of such a change could be of considerable significance biologically. It has been pointed out by Mysak (1986) that the occurrence of El Niño events has a large effect on the

migration habits of returning salmon, producing the northward diversion whereby Fraser River stocks choose to return via Johnstone Strait rather than the usual route through the Juan de Fuca Strait. Given such a response to temperature changes we must anticipate some response of the species to a secular warming trend, presumably a long-term tendency to return via the northern route. Since the coefficient of expansion of seawater is positive it follows that we must anticipate a rise in sea-levels in response to the warmer ocean environment. This has been discussed in a general way by Peltier and Tushingham (1989) and in an examination of trends at Station Papa in the Northeast Pacific Ocean by Thomson and Tabata (1989).

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Phototrophic Growth of Microalgae with Allantoic Acid or Hypoxanthine Serving as Nitrogen Source, Implications for Purine-N Utilization[1]

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Oliveira, L., and H. Huynh. 1990. Phototrophic growth of microalgae with allantoic acid or hypoxanthine serving as nitrogen source, implications for purine-N utilization. Can. J. Fish. Aquat. Sci. 47: 351–356.

Eleven species of marine phytoplankters assigned to seven different taxonomic divisions were tested for their ability to grow on hypoxanthine and some of its derivatives (allantoin, allantoate, urea) to study the mechanism of purine-N utilization in microalgae. All species tested were able to utilize urea, but only six of these were capable of growth on hypoxanthine. Growth on allantoic acid was restricted to six species, while no growth occurred with allantoin. In some species growth occurred only after supplementation of the culture media with Ni^{2+} or it was enhanced by it. These results suggested that purine-N utilization involved the production of urea and its subsequent conversion to utilizable ammonium by the enzyme urease. Demonstration of xanthine dehydrogenase, allantoinase, allantoicase, and urease activities in cell-free extracts of microalgae grown on hypoxanthine and of growth inhibition using the inhibitors allopurinol, 2,6,8-trichloropurine and hydroxyurea confirmed that urea is a major product of hypoxanthine degradation. However, in *Pavlova lutheri* growth in allantoate or hypoxanthine occurs in the presence of urease inhibitors. This suggests that the catabolic oxidation of purines and their derivatives does not always involve urea production and that purine-N utilization must be studied on a species basis.

Afin d'étudier le mécanisme d'utilisation du N sous forme de purine par les microalgues, la capacité que présentaient onze espèces de phytoplanctontes marins assignés à sept divisions taxonomiques différentes de croître sur l'hypoxanthine et quelques-uns de ces dérivés (allantoïne, allantoate, urée) a été évaluée. Toutes les espèces étudiées se sont montrées capables d'utiliser l'urée, mais seules six de ces espèces pouvaient croître sur l'hypoxanthine. De même, six espèces on pu être cultivées sur l'acide allantoïque et aucune espèce sur l'allantoïne. Dans certaines espèces, la croissance n'a pu se produire qu'après ajout au milieu de cultures de Ni^{2+}, ou bien s'en est trouvée améliorée. Ces résultats semblent indiquer que l'utilisation du N sous forme de purine comporte la production d'urée et sa conversion subséquente par l'uréase en ammonium utilisable. La démonstration qu'il existait des activités xanthine-déshydrogénase, allantoïnase, allantoïcase et uréase dans des extraits acellulaires de microalgues, cultivés sur hypoxanthine, ainsi qu'une inhibition de la croissance par les inhibiteurs allopurinol, 2, 6, 8-trichloropurine et hydroxyurée a confirmé que l'urée est un produit important de la dégradation de l'hypoxanthine. Cependant, chez *Pavlova lutheri*, la croissance dans l'allantoate ou l'hypoxanthine se produit en présence des inhibiteurs d'uréase. Cela semble montrer que l'oxydation catabolique des purines et de leurs dérivés ne comporte pas toujours la production d'urée et que l'utilisation du N sous forme de purine doit être étudiée pour chacune des espèces.

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Urea is an important source of organic nitrogen for phytoplankton growth (Anita et al. 1989) that can also be endogenously produced through metabolic pathways such as the aerobic degradation of purines (Naylor 1970). Recent studies on the phototrophic growth of several marine planktonic algae with urea serving as sole source of nitrogen showed that growth could only occur, in most cases, on addition of minute amounts of Ni^{2+} to the growth media (Oliveira and Antia 1984, 1986a). Of particular interest to these findings is the discovery that nickel is a constituent of the urease enzyme in jackbean (*Canavalia ensiformis* L., Dixon et al. 1975) and is required for urease activity in soybean tissue cultures (Polacco 1977). A nickel requirement for urease activity was also reported for some microalgae (Syrett 1981; Rees and Bekheet 1982; Oliveira and Antia 1986b).

Antia et al. (1989), in their review of the role of dissolved organic nitrogen in phytoplankton nutrition show widespread ability on the part of microalgae to utilize purines and/or their derivatives as sole sources of nitrogen. This is assumed to be related to the occurrence of a catabolic pathway of purine oxidation similar to that described in some microorganisms (Vogels and van der Drift 1976) and higher plants (Reynolds et al. 1982). The major feature of this pathway of purine oxidation is the formation of urea as the final product of purine-N degradation. However, as pointed out by Prasad (1983) and Antia et al. (1980a) the information available for the algae is at best fragmentary and restricted in most cases to test dealing exclusively

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TABLE 1. Species of microalgae used in the present study.

Species	Strain/clone (isolator/supplier/source)
Prymnesiophyceae	
Isochrysis galbana	Leftley, SMBA No. 58
Hymenomonas elongata	Leftley, SMBA No. 62
Prymnesium parvum	Droop, SMBA No. 65
Pavlova lutheri	Leftley, SMBA No. 261
Bacillariophyceae	
Thalassiosira nordenskioldii	Rao, Bedford Institute, Dartmouth, N.S.
Thalassiosira pseudonana	Neil Price, University of British Columbia
Chlorophyceae	
Dunaliella tertiolecta	Wood Hole Oceanographic Institution
Cyanophyceae	
Agemenellum quadruplicatum	Van Baalen, ATCC No. 27264
Dinophyceae	
Amphidinium carterae	J. McLachlan, NRC (Halifax, N.S.)
Chrysophyceae	
Olisthodiscus luteus	R. A. Cattolico, UW (Seattle, WA)
Eustigmatophyceae	
Nannochloropsis oculata	Leftley, SMBA, No. 66

with growth studies. Growth tests are further complicated by the fact that the concentration of Ni^{2+} in the culture media may influence the ability of the algae to utilize the intermediates of this pathway as sole source of nitrogen. Consequently, the mechanism(s) of purine-N utilization of marine microalgae is far from understood.

In this work, we report on the Ni^{2+} requirement of 11 species of marine phytoplankters belonging to seven different taxonomic divisions for growth on hypoxanthine, allantoin, allantoate or urea as sole source of N. Some of the species were previously reported unable to grow on some of these organic-N sources (Droop 1955; Conover 1975) and were included here to determine if Ni^{2+} was the limiting factor. Since recent evidence suggests that purine-N utilization may proceed in some higher plant cells without the production of urea (Winkler et al. 1987, 1988), we have also conducted growth inhibition and enzymatic studies to help elucidate the mechanism(s) of oxidation of purines and their derivatives responsible for the growth of these 11 species of microalgae.

Materials and Methods

Algal Species

Axenic cultures of 11 species of algae (Table 1) were routinely maintained on nitrate (as nitrogen source) using sterile conditions (Antia and Cheng 1970).

Growth Tests

Tests were carried out in culture tubes at 18°C under continuous illumination (irradiance 95–100 $\mu E \cdot m^{-2} \cdot s^{-1}$) from cool-white fluorescent lamps. The test medium was that of Oliveira and Antia (1984) with the salinity adjusted to 26‰. In the case of *Olisthodiscus luteus* and *Dunaliella tertiolecta*, final salinity of the test medium was retained at 14‰. Nitrogen sources included allantoin, allantoic acid, hypoxanthine, urea, or nitrate. The nitrogen stoichiometry for equivalent growth was defined by the equation 0.5 mM hypoxanthine ≡ 0.5 mM allantoin ≡ 0.5 mM allantoic acid ≡ 1 mM urea ≡ 2 mM nitrate (Oliveira and Antia 1984). All tests were conducted with (1 μM) or without Ni^{2+} supplementation of the culture media. Unless otherwise stated, 0.2-mL aliquots of experimental stock cultures were added to 4-mL of test media. Experimental stock cultures were obtained by growing the microalgae in the above mentioned nitrogen compounds prior to the removal of the inoculum. Growth inhibition studies were carried out by adding citrate (5 and 10 mM) or 0.5 to 500 μM of allopurinol, 2,6,8-trichloropurine or hydroxyurea to test media prior to inoculation. Three replicates were conducted for each experiment with the inoculum adjusted to the same cell count. All test media and inhibitor solutions were filter-sterilized (0.2-μm pore size presterilized Nalgene filters) and the test tubes autoclaved prior to inoculation. Aseptic techniques were used throughout the experiments to ensure axenic growth conditions.

Growth was monitored directly in culture tubes by periodically reading their optical density at 600 nm ($O.D.^{600}$) on a spectrophotometer after brief vortex mixing. Every growth test included a control without any added nitrogen source, and the growth measured on different nitrogen sources was corrected for the residual growth, if any, measured under those circumstances.

Enzyme Activities

Preparation of cell-free extracts of the microalgae for determination of enzyme activities was conducted according to the procedure described by Shah and Syrett (1984). Enzyme assays were carried out for xanthine dehydrogenase (Stirpe and Della Corte 1969), uricase (Theimer and Beevers 1971), allantoinase, allantoicase (Reinert and Marzluf 1975), and urease (Mackerras and Smith 1986). In some tests 1 to 10 μM of the inhibitors allopurinol, 2,6,8-trichloropurine, or hydroxyurea were added to cell-free extracts prior to incubation with the appropriate substrate. Three separate assays were performed for each enzyme activity tested. The reaction was stopped at regular time intervals by adding 0.1 mL of 10% (v/v) trichloroacetic acid to 1 mL of reaction mixture. The protein content of the extracts was determined by the method of Lowry et al. (1951) employing bovine serum albumin as a standard.

Results

Eleven species of microalgae representing different classes of phytoplankton were tested for their ability to utilize different components of the purine catabolism pathway, i.e. hypoxanthine, allantoin, allantoic acid or urea, as the sole source of nitrogen. These studies were conducted with (1 μM) or without the addition of Ni^{2+} to the culture media and the results (Table 2) show the concentrations required to obtain growth equivalent to that observed on nitrate (2 mM) controls. In the absence of Ni^{2+} addition all species, with the exception of *Amphidinium carterae* and *Olisthodiscus luteus*, were able to grow on urea. The addition of Ni^{2+} (1 μM) to the culture media was without effect on urea growth for the majority of the species tested, although in the case of *Hymenomonas elongata* and *Thalassiosira nordenskioldii* distinct improvement was observed. Both microalgae required lower concentrations of urea to achieve equivalent growth to the nitrate (2 mM) controls. A total nickel-dependency for growth on urea could only be demonstrated for

TABLE 2. Concentrations (mM) of urea, allantoic acid (Al ac), and hypoxanthine (hypox) required to support growth of the microalgae equivalent to that observed on nitrate (2mM) controls in the presence (1 μM) and absence of Ni^{2+} additions to the culture media. Symbol (—) indicates that the microalga does not grow in that particular N-source.

	Ni^{2+} (0 μM)			Ni^{2+} (1 μM)		
Species	Urea	Al ac	Hypox	Urea	Al Ac	Hypox
I. galbana	1.0	0.5	—	1.0	0.5	—
H. elongata	1.5	0.75	—	1.0	0.5	—
P. parvum	4.0	—	2.0	4.0	—	2.0
P. lutheri	1.0	0.5	0.5	1.0	0.5	0.5
T. nordenskioldii	2.0	—	—	1.0	—	—
T. pseudonana	1.0	—	—	1.0	—	—
D. tertiolecta	1.0	0.5	0.5	1.0	0.5	0.5
A. quadruplicatum	1.0	0.5	—	1.0	0.5	—
A. carterae	—	—	—	2.0	—	1.0
O. luteus	—	—	—	1.0	—	—
N. oculata	2.0	1.0	1.0	2.0	1.0	1.0

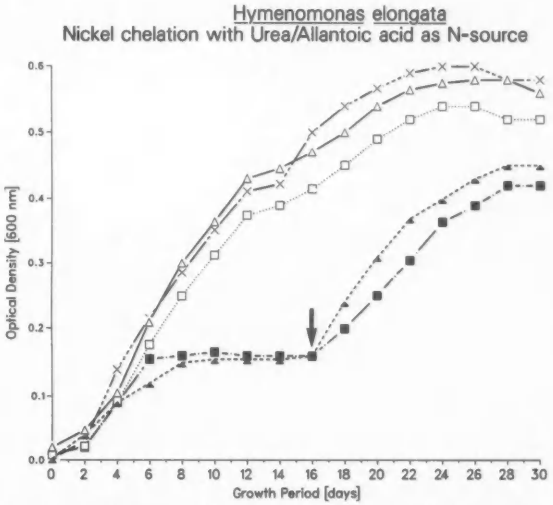

FIG. 1. Growth curves of *Hymenomonas elongata* in 24‰ salinity medium supplemented with Ni^{2+} (1 μM) and 2 mM nitrate without or with 5 mM citrate (×), 1 mM urea without (Δ) or with 5 mM citrate (▲), and 0.5 mM allantoate without (□), or with 5 mM citrate (■). Excess Ni^{2+} (1 μM) was added to citrate supplemented cultures at day 17 (arrow).

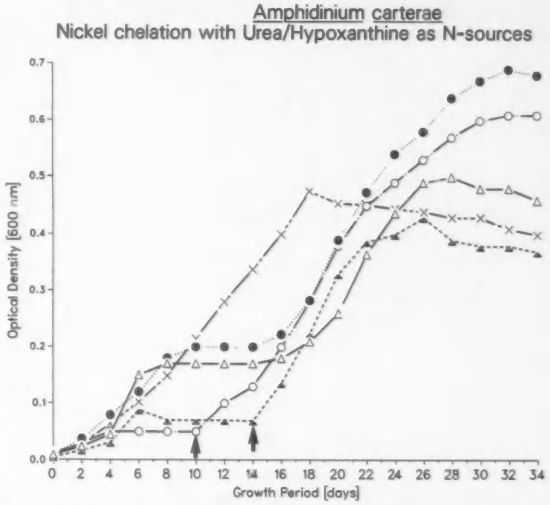

FIG. 2. Growth curves of *Amphidinium carterae* in 24‰ salinity medium supplemented with Ni^{2+} (1 μM) and 2 mM nitrate without or with 5 mM citrate (×), 1 mM urea without (Δ), or with 5 mM citrate (▲), 0.5 mM hypoxanthine without (●), or with 5 mM citrate (○). Excess Ni^{2+} (1 μM) was added to citrate supplemented cultures at days 10 and 14 (arrows).

TABLE 3. Concentrations (μM) of allopurinol (Al), 2,6,8-trichloropurine (Tc), and hydroxyurea (Hu) required for 50% inhibition of microalgal growth in media supplemented with hypoxanthine, allantoic acid, or urea as organic N-sources. Symbol (—) indicates that the microalga does not grow on that particular N-source.

	Organic N-source/inhibitors				
	Urea	Allantoic acid	Hypoxanthine		
Species	Hu	Hu	Al	Tc	Hu
I. galbana	1	1	—	—	—
H. elongata	10	10	—	—	—
P. parvum	10	—	1	5	10
P. lutheri	5	500	5	5	500
T. nordenskioldii	5	—	—	—	—
T. pseudonana	1	—	—	—	—
D. tertiolecta	500	500	2	5	500
A. quadruplicatum	10	10	—	—	—
A. carterae	1	—	1	10	1
O. luteus	5	—	—	—	—
N. oculata	10	10	1	10	10

Amphidinium carterae and *Olisthodiscus luteus* since no growth occurred in the absence of Ni^{2+} supplementation.

Growth on allantoic acid occurred in only six species. The concentration of allantoic acid required to produce growth equivalent to that on nitrate controls was half of that required when urea was used as sole source of nitrogen. The addition of Ni^{2+} to the culture media was without effect on the growth of the majority of the allantoic acid utilizers. The only exception was *Hymenomomas elongata* which was able to achieve equivalent growth to the nitrate control at a lower concentration of allantoic acid in Ni^{2+} supplemented medium (Table 2).

Of the 11 species tested, only five were able to grow on hypoxanthine as sole source of nitrogen. One of these species, *Amphidinium carterae*, showed a strict Ni requirement since no growth occurred in the absence of Ni^{2+} supplementation. The addition of Ni^{2+} to the culture media did not influence the growth of the other phytoplankters capable of utilizing hypoxanthine N. The concentration of hypoxanthine required to produce growth equivalent to that observed in nitrate controls was the same as that for allantoic acid growth in those species capable of utilizing either compound as nitrogen source. In every instance hypoxanthine concentration was half that required for equivalent urea growth (Table 2). None of the species tested was able to grow on allantoin as sole source of nitrogen.

Nickel chelation, using citrate as the chelator, was carried out to further study growth-dependency on this trace metal ion. In those organisms showing improvement or good growth on organic N-sources with nickel supplementation, growth was

TABLE 4. Xanthine dehydrogenase (XD), allantoinase (ALN), allantoicase (ALC), and urease (UR) activities in cell-free extracts of microalgae grown on hypoxanthine.

Species	Cell-free extract enzymatic activities[a]			
	XD	ALN	ALC	UR
P. parvum	1.6+0.3	2.1+0.2	1.7+0.1	1.6+0.2
P. lutheri	2.9+0.1	2.6+0.2	1.7+0.2	3.4+0.3
D. tertiolecta	2.2+0.3	3.0+0.2	1.5+0.3	—[b]
A. carterae[c]	3.1+0.2	1.9+0.3	2.3+0.1	4.1+0.3
N. oculata	2.0+0.2	2.3+0.2	2.1+0.2	2.4+0.2

[a]Enzyme activities (nmol product·min^{-1}·mg protein) represent averages +SD of three separate assays.
[b]Symbol (—) indicates absence of activity.
[c]Nickel (1 μM) added to the culture medium and cell free extract.

inhibited when citrate (5 mM) was added into the medium. The growth inhibition could be reversed by the addition of excess nickel (Figs. 1 and 2, arrows). In those microalgae that showed no requirement for nickel supplementation, the addition of citrate into the medium did not affect growth.

The growth inhibitors allopurinol, 2,6,8-trichloropurine, and hydroxyurea were added at various concentrations into media containing different organic N sources (Table 3). The urea-growth of all species of microalgae, with the exception of *Dunaliella tertiolecta*, was inhibited by hydroxyurea. Hydroxyurea-dependent inhibition of growth was also observed among those species capable of growing with allantoic acid and/or hypoxanthine, with the exception of *Dunaliella tertiolecta* and *Pavlova lutheri*. Growth inhibition occurred when 1.0 μM of allopurinol was added to hypoxanthine (nickel was added where required) cultures of *Prymnesium parvum, Amphidinium carterae*, and *Nannochloropsis oculata*. Slightly higher concentrations of allopurinol were required for *Pavlova lutheri* (5 μM) and *Dunaliella tertiolecta* (2 μM) in order for growth to be inhibited. A similar pattern of growth inhibition responses was also detected in these species when 2,6,8-trichloropurine was added to hypoxanthine-grown cultures.

Cell-free extracts of the microalgae were examined for xanthine dehydrogenase, uricase, allantoinase, allantoicase, and urease activities. All five species capable of growing on hypoxanthine N possessed most of these enzymatic activities when grown on this form of organic nitrogen (Table 4). The noticeable exceptions were uricase activity that could not be detected in cell-free extracts of all the microalgae tested and the absence of urease activity from cell-free extracts of *Dunaliella tertiolecta*. No inhibitors are known for allantoinase and allantoicase activities, but in the case of xanthine dehydrogenase, inhibition of activity can be demonstrated in cell-free extracts by utilizing allopurinol (Fig. 3).

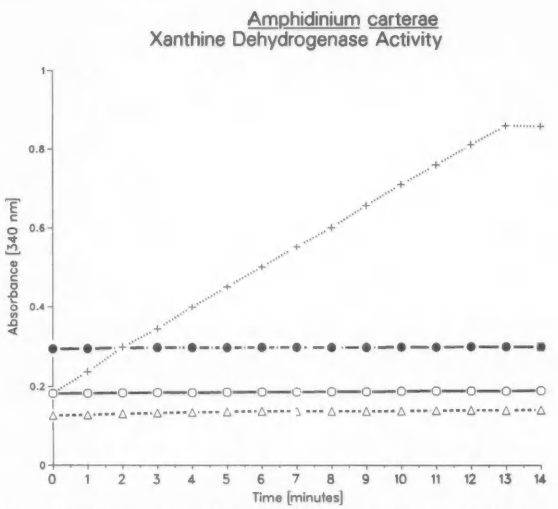

FIG. 3. Inhibition of xanthine dehydrogenase activity of cell-free extracts of *Amphidinium carterae* with allopurinol. Reaction mixture (1 mL) with cell-free extract (○), cell-free extract plus 1 μM allopurinol (Δ), cell-free extract plus 1 mM hypoxanthine (+), and cell-free extract plus 1 mM hypoxanthine plus 1 μM allopurinol (●).

Discussion

The facility and efficiency of urea utilization by most of the species surveyed confirm the findings of previous authors that urea is one of the most important sources of organic-N available for growth of marine phytoplankton (see Oliveira and Antia 1984 for review). The available evidence, on the distribution of urea-degrading enzymes, indicates that two alternative enzyme systems (urease and ATP:urea amidolyase) occur in algae. ATP:urea amidolyase is restricted to some members of the Chlorophyceae, while urease occurs in all other algal classes and some of the chlorophycean algae examined so far (Leftley and Syrett 1973; Bekheet and Syrett 1977; Syrett 1981; Al-Houty and Syrett 1984). More germane to this problem was the identification of nickel as a constituent of jackbean (*Canavalia ensiformis* L.) urease (Dixon et al. 1975) and soybean tissue cultures (Polacco 1977). A nickel requirement for urease activity was also reported for some microalgae (Syrett 1981; Rees and Bekheet 1982; Oliveira and Antia 1986b). Therefore, the strict requirement for Ni^{2+} exhibited by *Amphidinium carterae* and *Olisthodiscus luteus* for growth on urea as sole source of organic-N suggests that urease is the enzyme responsible for the conversion of urea into utilizable ammonium (Polacco 1977). This is confirmed by both the hydroxyurea- and citrate-dependent growth inhibitions observed when these microalgae are supplemented with urea as sole source of nitrogen.

The endogenous nickel content of the sea water used in the preparation of our test media is 3.42 nM and the endogenous nickel in the final media, excluding contamination from added salts, is in the order of 2.7 and 1.4 nM for the salinities of 26 and 14‰ utilized in the present study, respectively (Oliveira and Antia 1984). The growth enhancement observed in urea-grown cells of *Hymenomonas elongata* and *Thalassiosira nordenskioldii* with nickel supplementation, therefore, implies that urease also occurs in these microalgae. This is further confirmed by the strong growth inhibition observed when citrate, the natural Ni^{2+}-chelator found in nickel accumulating plants (Kersten et al. 1980), is added to the culture media. In contrast, the growth of *Pavlova lutheri, Dunaliella tertiolecta, Agmenellum quadruplicatum, Isochrysis galbana*, and *Nannochloropsis oculata* on urea displayed no signs of nickel requirement. Furthermore, the addition of citrate did not affect the growth of these organisms. These data suggest that either these organisms have the capacity to readily concentrate Ni^{2+} from the nanomole levels normally occurring in seawater (see Oliveira and Antia 1986a for review) or they use the ATP:urea amidolyase Ni^{2+}-independent system for the conversion of urea

directly to utilizable ammonium (Oliveira and Antia 1986b). In the case of *Pavlova lutheri, Agmenellum quadruplicatum, Isochrysis galbana*, and *Nannochloropsis oculata*, the first explanation is more likely, since growth of these microalgae in urea as sole source of nitrogen is inhibited by hydroxyurea, a potent inhibitor of urease activity (Reithel 1971; Carvajal et al. 1982) and urease was detected in these microalgae. These compounds are without effect on the urea-supported growth of *Dunaliella tertiolecta*. Instead, this is inhibited by avidin, a known inhibitor of ATP:urea amidolyase activity. Furthermore, addition of biotin abolishes the avidin-induced inhibition (L. Oliveira, unpubl. data). These results are indicative of the occurrence of ATP:urea amidolyase activity and explains the reason why a nickel requirement is absent from this microalga (Leftley and Syrett 1973; Carvajal et al. 1982).

According to Antia et al. (1989), allantoic acid has not been previously tested as an organic-N source for the growth of microalgae. Under our test conditions, only six of the 11 species studied grew on this nitrogen source. Since the N-atoms stoichiometry of allantoic acid versus urea is 4:2, the results suggest that these microalgae utilize the allantoic acid N as efficiently as that from urea. These results may then be construed to imply that allantoic acid might be catabolized to urea and ureidoglycolate by the enzyme allantoicase (Antia et al. 1989; Shah and Syrett 1984). This is supported by the determination of allantoicase activity in cell-free extracts of some of these microalgae (Table 3). The inhibition of allantoate-supplemented cultures of *Agmenellum quadruplicatum, Hymenomonas elongata, Isochrysis galbana*, and *Nannochloropsis oculata* by hydroxyurea further supports this interpretation. However, the absence of inhibition displayed by allantoate-grown cells of *Pavlova lutheri* treated with hydroxyurea suggests that in this case urea might not be one of the products of the catabolic action of this enzyme. Hydroxyurea also showed no effect upon the growth of allantoate-supplemented cultures of *Dunaliella tertiolecta*. However, these results are not surprising since ATP:urea amidolyase, not urease, was shown to be the enzyme responsible for the catabolic metabolization of urea-N in this genus (Leftley and Syrett 1973). The nickel-independence of ATP:urea amidolyase explains the absence of Ni^{2+}-requirement for growth on this and other urea-producing sources of organic N (Oliveira and Antia 1986b). Nickel-independence was also demonstrated in allantoic acid grown cultures of *Pavlova lutheri, Agmenellum quadruplicatum, Isochrysis galbana*, and *Nannochloropsis oculata*. In contrast, *Hymenomonas elongata* was able to achieve equivalent growth to the nitrate control at a lower concentration of allantoic acid and the addition of citrate to allantoic acid supplemented cultures suppressed growth. These results suggest that this metal ion is required for growth of *Hymenomonas elongata* in this organic-N source.

Allantoin was also tested for its ability to support the growth of phytoplankton as the sole source of organic-N. No growth was observed in all species studied. This confirms Antia et al. (1980b) observations suggesting that this form of organic-N is generally a poor N-source for phytoplankton growth relative to the purines. Although the possibility was not tested in the present study, Ammann and Lynch (1964) suggested that a cellular permeability barrier to allantoin might be the cause of the absence of growth.

Hypoxanthine was chosen as the prime purine representative for this investigation not only on account of its established stability in natural sea water (Antia and Landymore 1974; Antia et al. 1975) but also because unlike adenine or guanine, it does not possess any exocyclic nitrogenous group; hence any nitrogen utilization must depend on the ability of a particular species to retrieve the purine-skeleton nitrogen (Antia et al. 1989). Of the 11 species examined in this investigation, only five grew on hypoxanthine. Since both hypoxanthine and allantoic acid contain 4 N atoms versus 2 N atoms per molecule of urea, the evidence indicates that these microalgae are efficient utilizers of all the hypoxanthine-N. With the exception of *Amphidinium carterae*, hypoxanthine growth was not dependent upon Ni^{2+} supplementation and proceeded in the presence of the Ni^{2+} chelator citrate. The addition of citrate to hypoxanthine-cultures of *Amphidinium carterae* suppressed growth. The growth suppression was reversible, since the addition of excess nickel into the culture medium restored it. These data further support the nickel-dependency of this process and confirm that urease is the enzyme responsible for urea catabolism in this microalga.

As reported by Fujihara and Yamaguchi (1978), allopurinol [4-hydroxypyrazolo (3,4-d) pyrimidine], an analogue of hypoxanthine, is a potent inhibitor of the enzyme xanthine dehydrogenase. This enzyme is responsible for the oxidation of hypoxanthine to xanthine, and this to uric acid (Antia et al. 1989). Therefore, the growth inhibition observed in hypoxanthine to xanthine, and this to uric acid (Antia et al. 1989). Therefore, the growth inhibition observed in hypoxanthine-grown cultures of *Prymnesium parvum, Pavlova lutheri, Dunaliella tertiolecta, Amphidinium carterae*, and *Nannochloropsis oculata*, when allopurinol was added into the culture medium, implies that the degradation of hypoxanthine → xanthine → uric acid is dependent on the activity of xanthine dehydrogenase. The demonstration of the occurrence of xanthine dehydrogenase activity in these microalgae confirms this interpretation (Table 4).

Uricase (urate:oxygen oxidoreductase) is a cuproprotein that catalyzes the oxidation of urate in the presence of oxygen, yielding hydrogen peroxide (H_2O_2), carbon dioxide, and allantoin (Mahler et al. 1955). A number of substances are known to be effective inhibitors of uricase. These include oxypurines, 2,6,8-trichloropurine and oxonate (Muller and Moller 1969 and references cited therein). The growth inhibition of hypoxanthine-supplemented cultures of these microalgae, treated with trichloropurine, indicates that uricase is responsible for the uric acid → allantoin catalytic conversion. Failure to detect uricase activity in crude cell-free extracts of the microalgae may be related to the high sensitivity of this enzyme to changes in pH, among other factors (Oliveira and Huynh 1989b). Indeed, Shah and Syrett (1984) also failed to detect uricase activity in crude extracts of the marine diatom *Phaeodactylum tricornutum*, although activity was measurable in partially purified fractions of the extract. Urate oxidation proceeds simultaneously with the degradation by catalase of the H_2O_2 formed during the reaction. It is then important to notice that cytochemical studies of *Amphidinium carterae, Dunaliella tertiolecta*, and *Pavlova lutheri* reveal the occurrence of both uricase and catalase activities (Oliveira and Huynh 1989a, b). The determination in crude cell preparations of the microalgae of allantoinase and allantoicase activities suggests then that a pathway of purine degradation responsible for the utilization of the nitrogen of purines and its derivatives via urea production also occurs in these microalgae (Vogels and van der Drift 1976; Reynolds et al. 1982). The fact that urease inhibitors, with the exception of *Dunaliella tertiolecta* and *Pavlova lutheri*, block the growth of hypoxanthine-supplemented cultures of the other three species

able to grow on this N source further supports this interpretation. The lack of hypoxanthine-growth inhibition of *Dunaliella tertiolecta* by urease inhibitors reflects the occurrence of ATP:urea amidolyase activity (Leftley and Syrett 1973). The fact that utilization of hypoxanthine and allantoic acid by *Pavlova lutheri* remains unaffected in the presence of urease inhibitors suggests that the catabolic oxidation of purines and their derivatives does not involve the production of urea. Recently Winkler et al. (1987, 1988) showed that allantoin catabolism in soybean suspension culture cells is carried out by two amidohydrolase reactions, allantoate amidohydrolase and ureidoglycolate amidohydrolase, and that the whole process proceeds without detectable production of urea. The ability for urea utilization exhibited by *Pavlova lutheri* may then represent a system independent from that of purine catabolism, such as that of the ornithine cycle involving urea release from arginine by arginase (Naylor 1970). The detection of urease activity in hypoxanthine-grown cells is consistent with this possibility. However, whether or not a two amidohydrolase system similar to the one observed in soybean exists in *Pavlova lutheri* remains to be determined.

In conclusion, some microalgae possess the ability to utilize purines and/or its derivatives as sole source of N. The catabolic oxidation of these compounds seems to occur in most of these microalgae by a pathway of purine oxidation similar to the one described for other microorganisms (Vogels and van der Drift 1976) and higher plants (Reynolds et al. 1982). However, in the case of the Prymnesiophyte *Pavlova lutheri*, oxidation of purines seems to take place without final conversion to urea. This indicates the occurrence in this microalga of a modification of the pathway of purine-N utilization (Antia et al. 1989) and resembles the situation reported for soybean suspension cell cultures (Winkler et al. 1987, 1988). Laboratory tests are now in progress to eludicate this mechanism.

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Patterns in the Submerged Macrophyte Biomass of Lakes and the Importance of the Scale of Analysis in the Interpretation[1]

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Duarte, C. M., and J. Kalff. 1990. Patterns in the submerged macrophyte biomass of lakes and the importance of the scale of analysis in the interpretation. Can. J. Fish. Aquat. Sci. 47: 357–363.

The relative contributions of lake characteristics (i.e. alkalinity, chlorophyll *A* concentration, total phosphorus concentration, conductivity, and morphometry) and site characteristics (i.e. depth, littoral slope, exposure to waves, and underwater light levels) to the variability in submerged biomass were examined in 25 Canadian and American lakes. Lake-average submerged biomass is a function of water alkalinity and the lake-average littoral slope whereas site-specific biomass is a function of both site and lake characteristics. Plant biomass decreased with increasing slope and wave exposure and increased with increasing alkalinity and light levels. However, these relationships are complex because submerged biomass is also influenced by threshold phenomena (e.g. critical littoral slopes and transparency-dependent critical depths) that set limits to macrophyte colonization and because the relative contributions of the most relevant environmental factors studied (i.e. littoral slope, exposure, water transparency, and alkalinity) are depth dependent. By demonstrating the importance of lake-average and site-specific scales of variation and the existence of noncontinuous (e.g. threshold) regulation mechanisms the findings provide a new conceptual framework for the study of the relationship between submerged macrophytes, and their associated biota as well as their environment.

Vingt-cinq lacs du Canada et des États-Unis ont été étudiés afin que soit mesurée la contribution relative sur la variabilité de la biomasse submergée, des caractéristiques d'ensemble des lacs (alcalinité, concentration en chlorophylle *a*, concentration en phosphore total, conductivité, morphométrie) ainsi que des caractéristiques de stations précises (profondeur, pente du rivage, exposition aux vagues, luminosité sous l'eau). Pour chaque lac, la biomasse submergée moyenne pondérée sur la superficie totale est une fonction de l'alcalinité de l'eau et de la pente moyenne du rivage (sur l'ensemble du périmètre du lac), alors que la biomasse à des stations précises est une fonction des caractéristiques de la station ainsi que des caractéristiques du lac. Plus la pente est forte et plus l'exposition aux vagues est grande, moins il y a de biomasse végétale; plus l'alcalinité est élevée et plus il y a de lumière, plus il y a de biomasse. Cependant, ces rapports sont complexes car la biomasse submergée est aussi influencée par des phénomènes-seuils (p. ex., des pentes de rivage critiques et des profondeurs critiques associées à la limpidité de l'eau) qui déterminent des limites à la colonisation par les plantes macrophytes; cette complexité tient aussi au fait que la contribution relative des facteurs du milieu les plus déterminants qui ont été étudiés (c.-à-d. la pente de rivage, l'exposition, la limpidité de l'eau et l'alcalinité) sont fonction de la profondeur. Les résultats obtenus permettent d'étudier sous un éclairage nouveau la relation entre les plantes macrophytes submergées et leurs biotes associés ainsi que leur milieu, car ils montrent quelle est l'importance des échelles de variations observées à des endroits précis et pondérées sur la superficie totale de chacun des lacs considérés et qu'ils montrent l'existence de mécanismes régulateurs qui n'agissent pas de manière continuelle (p. ex., l'existence de seuils).

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Macrophyte ecologists have not yet reached a consensus on the relative importance of different environmental factors in determining the biomass of submerged macrophytes in lakes. Studies that compare submerged macrophyte growth among lakes normally conclude that chemical (e.g. dissolved inorganic carbon) and trophic factors control macrophyte growth (e.g. Spence 1967; Adams et al. 1978) whereas those that focus on local differences in biomass point to differences in depth (Spence 1982), wave exposure, littoral slope (Duarte and Kalff 1986), and sediment characteristics (Anderson and Kalff 1986) as key factors. These different conclusions may not be in conflict because it may well be that the nature and importance of different factors controlling the submerged macrophyte biomass change with the scale of analysis.

The variability of lake water chemistry and trophic status within individual lakes is much smaller than that among lakes (cf. Forsberg and Heyman 1984) whereas site characteristics (e.g. exposure to waves, slope, and sediment characteristics) may change as much within as among lakes (e.g. Duarte and Kalff 1986). Therefore, water chemistry and trophic characteristics should be important in explaining differences in macrophyte biomass among lakes whereas site characteristics should be important in explaining biomass variability within lakes. Consequently, comparisons based on lake-average biomass are unlikely to reveal any influence of site characteristics whereas studies based on changes in macrophyte biomass around the littoral zone of individual lakes would fail to demonstrate the importance of water chemistry and trophic state.

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Here we attempt to unify apparently divergent views on the regulation of submerged macrophyte biomass in lakes by showing that the relationships between submerged macrophyte biomass and environmental variables differ with the scale of analysis used. We do this by collecting data on both macrophyte biomass and lake plus site characteristics from 25 northeastern North American lakes. We first describe the relationship between both lake-average biomass and site-specific biomass and the measured environmental variables. We then propose a new conceptual framework for the study of biomass variability that may help to alleviate grounds for disagreement on the relationships between macrophytes biomass and environmental characteristics by researchers who are in fact examining these relationships at different scales.

Macrophyte biomass was measured at multiple sites within each lake, and the environmental characteristics used included lake trophic status (represented by the epilimnetic chlorophyll *a* and total phosphorus concentrations), lake morphometry (represented by the lake area and maximum and mean depths), the major ion chemistry of the lakes (represented by epilimnetic conductivity and alkalinity), rooting depth, littoral slope, and exposure to waves.

Study Lakes

The study involved 25 lakes in Quebec, New York, and Vermont (Table 1), selected to cover the widest range in environmental factors within that region. The lakes in this study are of glacial origin, with the exception of a single reservoir (L. Boivin). Their catchments vary from totally forested and unaffected by direct human influence (e.g., L. Cromwell, L. Montjoie), to lakes that support some recreational use (e.g. L. George, L. Memphremagog), and lakes heavily influenced by wastewater inputs (e.g. L. Boivin, L. Waterloo). The lakes ranged in size from the large Missisquoi Bay (L. Champlain, Table 1) to lakes of only a few hectares (L. Cromwell, Table 1). The lakes also varied from oligotrophic (e.g. L. George, L. Bowker) to eutrophic (e.g. L. Boivin, L. Waterloo, Table 1).

Methods

The biomass of submerged macrophytes was measured in August 1985, the time of maximum biomass in the area, using relationships between plant biomass and vegetation height derived from echosounder tracings and plant growth form (Duarte 1987). At each lake we selected 4 — 38 (depending on lake size) sampling transects (total sampling transects = 187) selected to cover the widest possible range of littoral morphometry. At each sampling transect site, a recording echosounder (Si-tex Honda, model HE-356) was used to obtain six replicated echosounding transects perpendicular to shore within 5–10 m of each other between a depth of about 0.5 m and the vegetation limit. These were also used to record the dominant macrophyte growth form along the transects (cf. Duarte 1987). For each replicated transect the vegetation height was obtained from the echograms at 7- to 9-m intervals. Submerged biomass for the site was then calculated from the average vegetation height and the dominant plant growth form at each interval using the equations in Duarte (1987). This process yielded biomass estimates for over 8000 intervals, which were reduced to 1400 biomass estimates by averaging the observations over 0.5-m depth classes (N = 3–15 individual intervals per estimate). These values are hereafter referred to as "site" biomass, where site refers to an area of about 50–100 m^2. Our study, therefore, ignores variation occurring at smaller (i.e. within-site) spatial scales that appears to result from neighbor interactions and sediment heterogeneity (Anderson and Kalff 1986).

TABLE 1. Limnological characteristics of the lakes studied, range of macrophyte biomass, and dominant species. *P.* = *Potamogeton; M* = *Myriophyllum; E.* = *Elodea; V.* = *Vallisneria; I.* = *Isoetes.*

Lake	Lat.	Long.	Area (ha)	Z_{max} (m)	Z_{mean} (m)	Cond. ($\mu S \cdot cm^{-1}$)	Alk. (mg $CaCO_3 \cdot L^{-1}$)	Secchi (m)	Chl *a* ($mg \cdot m^{-3}$)	TP ($mg \cdot m^{-3}$)	Dominant species
Bleu	45°55′	73°56′	1	6	—	35	7	4.2	—	—	*P. foliosus*
Boivin	45°23′	72°45′	160	6	2	321	78	0.6	15.2	125	*M. spicatum*
Bowker	45°25′	72°13′	230	59	26	48	18	7.8	1.0	10	*P. robinsii/I. lacustris*
Brome	45°15′	72°30′	1 452	13	6	89	32	3.7	2.0	13	*V. americana*
Brompton	45°26′	72°09′	1 191	42	12	59	22	4.2	1.2	3	*P. praelongus*
Brompton (Little)	45°26′	72°06′	67	20	8	63	28	3.6	2.0	6	*V. americana/I. lacustris*
Conneley	45°54′	73°58′	129	22	8	96	22	5.1	1.5	9	*P. praelongus*
Croche	45°54′	73°10′	39	10	9	29	9	4.0	1.6	10	
Cromwell	45°59′	73°09′	11	18	3	35	10	2.4	8.6	11	*P. praelongus*
D'Argent	45°18′	72°18′	96	16	5	87	31	3.1	3.5	14	*M. spicatum/P. praelongus*
George	45°30′	73°40′	11 000	59	18	90	24	8.5	0.6	8	*M. spicatum/P. amplifolious*
Hertel	45°32′	73°09′	29	8	5	86	50	3.8	3	10	*P. perfoliatus/P. robinsii*
Lovering	45°10′	72°09′	464	25	10	57	24	2.8	2.1	16	*M. exalbescens/Nitella* sp.
Magog	45°15′	72°10′	1 080	19	10	165	50	2.5	9.3	40	*M. spicatum/E. canadensis*
Massawippi	45°13′	72°00′	1 790	85	40	140	70	4.5	4.6	16	*M. spicatum*
Memphremagog	45°14′	72°14′	9 010	108	18	145	45	4	6.8	9	*M. spicatum/P. robinsii*
Missisquoi Bay	45°03′	73°09′	7 750	4	3	94	27	1.8	10	65	*M. spicatum*
Montjoie	45°24′	72°05′	329	22	8	36	18	3.2	0.8	8	*P. foliosus*
Orford	45°18′	72°16′	122	48	18	226	40	8	0.6	1	*P. praelongus*
Roxton Pond	45°28′	72°39′	179	5	3	120	39	2.9	4.1	18	*M. spicatum*
Selby	45°53′	72°47′	111	8	3	160	49	2.7	7.2	11	*M. spicatum*
Silver	45°38′	72°48′	68	62	27	110	35	5.8	3.5	8	*E. canadensis*
Stukely	45°22′	72°15′	386	32	14	49	24	6.5	0.8	3	*P. perfoliatus*
Trousers	45°14′	72°20′	60	13	7	55	15	2	1.1	7	*P. species*
Waterloo	45°20′	72°05′	150	5	3	147	44	0.8	23.7	34	*M. spicatum/V. americana*

Lake area and mean depth were obtained from bathymetric maps, and wave exposure was estimated from the area (square kilometres) of open water exposed at each site (Duarte and Kalff 1988). Littoral slope was measured from echosounder tracings as the slope between the beginning and end of each transect. Water samples were obtained from duplicated integrated epilimnetic water samples. These were collected with a sampling tube extended to the thermocline in the pelagic zone of each lake, or to 0.5 m from the bottom in unstratified lakes. The water was analyzed for total phosphorus following persulfate digestion, modified after Johnson (1971). Chlorophyll *a*, uncorrected for pheophytin, was determined after filtering between 0.5 and 1 L of water through 0.4-μm Gelman membrane filters, followed by ethanol extraction (Sartory and Grobbelaar 1984) and spectrophotometric determination. Electric conductivity was measured in surface waters with a model PCM1 Cole-Parmer meter with readings corrected to 25°. Water transparency was measured with a 20-cm-diameter Secchi disc. The percent surface irradiance (S_i) reaching the depth of growth (z) as measured from the echosounder tracings was calculated as $S_i = 100\ e^{-zk}$, where k was estimated as 1.47/Secchi transparency (Walker 1982). The major ion chemistry of the water was obtained from published reports (Service de la qualité des eaux 1978; Provencher et al. 1979; Henson and Gruendling 1977; Lafond 1985; Long et al. 1981).

The relationships between environmental factors and submerged biomass were described using linear regression analysis. The dependent and independent variables were transformed when necessary to meet requirements of linear regression, and the reduction in mean square error was used to choose between alternative models. Where needed, the data were split into groups to minimize the mean square error (Breiman et al. 1984; Duarte and Kalff 1986).

Results

Lake and Site Characteristics

The lakes sampled ranged widely in size, trophic status, and dominant macrophyte species (Table 1). The smallest ranges were those for total alkalinity and electrical conductivity (Table 1), reflecting the dominance of igneous and metamorphic geologies in northeastern North America. The lakes also differed in their light attenuation characteristics, from lakes where light attenuation was largely a function of algal biomass (e.g. L. Memphremagog) to highly colored lakes (e.g. L. Cromwell). The lake-average littoral slope differed considerably among lakes (Table 2), some lakes having very steep littorals (e.g. L. Bowker, L. Brompton, Table 2), some others very gentle ones (e.g. L. Selby, Roxton Pond, Table 2), and yet others a wide range of littoral zone slopes (e.g. L. George, Table 2). The exposure of sites to waves varied widely, but its variation within lakes was small (Table 2) because exposure was largely a function of lake size ($r = 0.90$).

The diversity in littoral and lake characteristics was matched by a great variation in submerged plant biomass both among and within lakes (Table 2). The biomass variance was as large within some lakes (e.g. L. Massawippi, Table 2) as the overall variance, indicating that the factors that generated biomass variation within lakes (e.g. littoral morphometry) were at least as important as those that created differences among lakes. This was supported by the positive correlation between the variability in submerged biomass within lakes (as the coefficient of variation) and the corresponding variability in littoral slope ($r = 0.45$, $P < 0.01$).

TABLE 2. Mean and coefficient of variation of the biomass, slope, and exposure to waves in the littoral of the different lakes.

	Slope (%)		Exposure (km^2)		Biomass (g fresh wt·m^{-2})	
Lake	Mean	C.V.	Mean	C.V.	Mean	C.V.
Bleu	14.9	88.1	0.08	44.2	5	11
Boivin	6.9	166.3	0.36	38.9	300	326
Bowker	41.2	76.0	0.16	87.5	10	23
Brome	2.8	39.2	11.62	15.6	42	25
Brompton	20.1	48.1	0.21	20.0	2	4
Brompton (Little)	5.2	115.6	7.62	36.0	23	230
Conneley	17.6	145.4	0.73	25.8	116	176
Croche	20.8	37.4	0.39	0.3	0	0
Cromwell	9.2	40.2	0.11	1.8	50	117
D'Argent	12.0	101.7	0.86	2.2	138	155
George	7.5	139.0	18.46	84.1	114	167
Hertel	3.6	91.6	0.28	3.2	504	494
Lovering	4.1	78.4	2.55	80.0	40	44
Magog	2.4	50.6	3.19	44.8	439	323
Massawippi	4.9	110.9	5.44	59.9	514	684
Memphremagog	8.3	76.9	11.17	94.4	206	229
Missisquoi Bay	2.6	66.8	42.90	43.1	90	87
Montjoie	9.2	63.2	3.29	0.6	1	2
Orford	5.7	51.5	0.71	64.8	72	47
Roxton Pond	1.5	33.3	2.60	0.5	606	168
Selby	2.2	27.8	0.39	0.8	1113	141
Silver	13.2	66.1	0.57	33.3	45	78
Stukely	8.0	83.2	1.45	33.6	10	18
Trousers	16.2	56.6	0.09	75.3	8	16
Waterloo	2.8	130.3	0.70	34.2	212	282

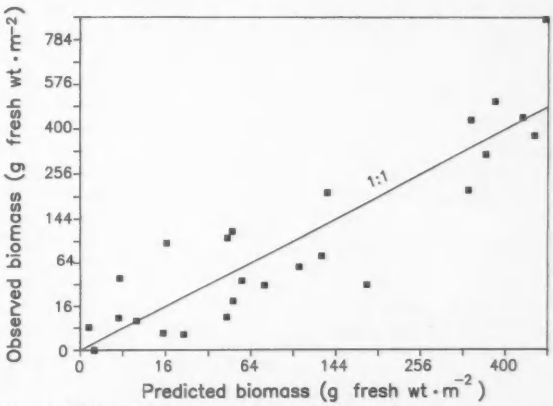

FIG. 1. Relationship between the mean biomass of submerged macrophytes and that predicted from alkalinity and the average slope (Eq. 1).

Patterns in the Lake-Average Biomass of Submerged Macrophytes

The mean biomass of submerged macrophytes in the lakes, estimated as the average of all biomass estimates (N = 54–280 sites per lake), was strongly correlated with the lake-average littoral slope and with the water alkalinity (Fig. 1). The best model to describe this relationship was

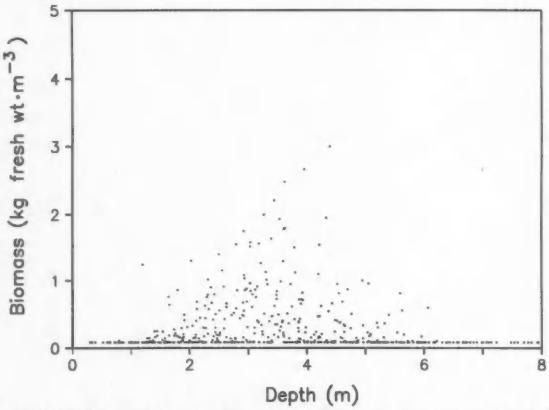

FIG. 2. Depth profiles of submerged macrophyte biomass constructed by pooling the data for all sites.

$$(1)\quad \text{Biomass}^{0.5} = -2.2 - 0.6\ \text{slope}^{-0.81} + 0.8\ (\text{alkalinity/slope})^{0.5}$$
$$(R^2 = 0.80\ P < 0.0001,\ \text{SE}_{(\text{estimate})+(0.5)} = 3.7)$$

where biomass is measured in grams fresh weight per square metre, slope as the depth change per unit horizontal distance (in metres), and alkalinity in milligrams per litre as $CaCO_3$.

Submerged macrophyte biomass was positively correlated with lake trophic status, both as chlorophyll *a* ($r = 0.58$, $P < 0.05$) and total phosphorus ($r = 0.40$, $P < 0.05$). However, total alkalinity and electrical conductivity were themselves significantly ($P < 0.05$) correlated with total phosphorus and chlorophyll *a*, so that the interpretation of the correlation between macrophyte biomass and lake trophic status is ambiguous (cf. Hutchinson 1975). However, the relationship between biomass and alkalinity ($r = 0.80$, $P < 0.001$, Fig. 2) was stronger than those to conductivity ($r = 0.72$, $P < 0.01$) or lake trophic status. Furthermore, the partial correlation of submerged biomass to alkalinity (after considering littoral slope) was highly significant ($P < 0.001$) whereas those to total phosphorus and conductivity were not ($P > 0.05$).

Patterns in the Site-Specific Biomass of Submerged Macrophytes

The relationship between lake-average macrophyte biomass and alkalinity indicated that water chemistry set one kind of a limit to the biomass production in the lakes. This limit, combined with restrictions on macrophyte growth imposed by site-specific conditions, probably accounted for the variability in submerged biomass among the sites visited. We used stepwise linear regression analysis to describe the relationship between site-specific biomass, as the dependent variable, and environmental characteristics of the lake (i.e. alkalinity, chlorophyll *a*, total phosphorus, conductivity, and transparency) and of the sites (i.e. slope, wave exposure, and depth) as independent variables. This procedure resulted in a model with 12 highly significant (*F*-test), $P < 0.001$) terms (comprising interactions of slope, exposure to waves, water transparency, water alkalinity, and a polynomial expression of depth) explaining approximately 40% of the biomass variance. Although the complexity of the regression model obtained reflects the complexity of the littoral zone, it serves our purposes poorly because (1) it obscures a comprehensible view of the littoral zone and (2) the relationship of submerged biomass to the individual factors is difficult to extract from the conglomerate of simultaneous changes and interactions. We therefore attempted to provide a more comprehensible description of the relationship between site-specific submerged biomass and environmental conditions by extracting the following simple patterns.

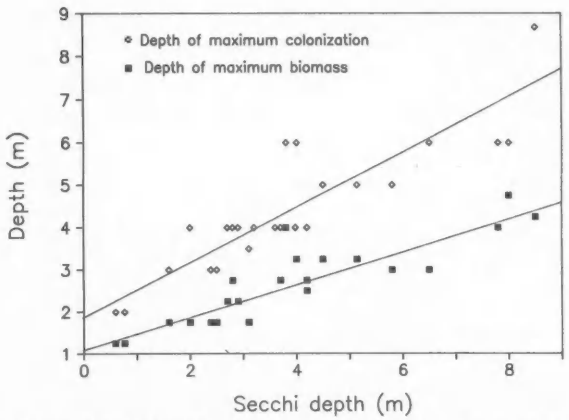

FIG. 3. Relationships between the depth of maximum colonization (Z_{mc}, Eq. 2) and the depth of maximum biomass (Z_{mb}, Eq. 3) of submerged macrophytes and the water transparency. The lines shown represent the regression equations (Eq. 2 and 3).

The depth distribution of submerged biomass had a parabolic shape in all lakes, which results in a parabolic envelope enclosing all of the depth–biomass combinations (Fig. 2). Individual transects typically had a biomass maximum at an intermediate depth, decreasing towards either side of the maximum (Fig. 2). This pattern has been suggested to result from the interaction of the stress produced by physical disturbance at shallow depths and light attenuation below the depth of maximum biomass (Spence 1982). The position of the biomass maximum and deepwater minimum are strongly related to the water transparency because both the average depth of maximum colonization (Z_{mc}) and the average depth where the maximum biomass occurs (Z_{mb}) are functions of the water transparency (Fig. 3):

$$(2)\quad Z_{mc}\ (\text{m}) = 1.9 + 0.63\ \text{Secchi (m)}\ (R^2 = 0.76,\ P < 0.0001)$$

$$(3)\quad Z_{mb}\ (\text{m}) = 1.1 + 0.4\ \text{Secchi (m)}\ (R^2 = 0.79,\ P < 0.0001).$$

These relationships are stronger than those previously reported (Chambers and Kalff 1985; Canfield et al. 1985), likely because the large number of transects examined within each lake reduces the uncertainty around the average estimates to levels close to the error around the regression estimates. The use of lake-average depths of maximum biomass and maximum colonization is probably the reason for the shallower depths calculated with Eq. 2 and 3 than those calculated using the models in Chambers and Kalff (1985), who used not the average but the deepest of the maximum depths of colonization observed in a series of transects. The shallowest depth where submerged vegetation grew (0.75–1.25 m) was not related ($P > 0.05$) to slope, wave exposure, or transparency, even though Chambers (1987) found such a correlation with wave exposure for four of the present lakes. Because a biomass increase below the shallow biomass

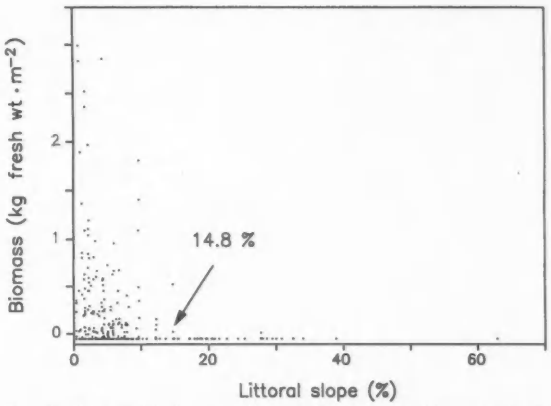

FIG. 4. Relationship between littoral slope and the biomass of submerged macrophytes, showing the value of the critical slope above which plants do not grow.

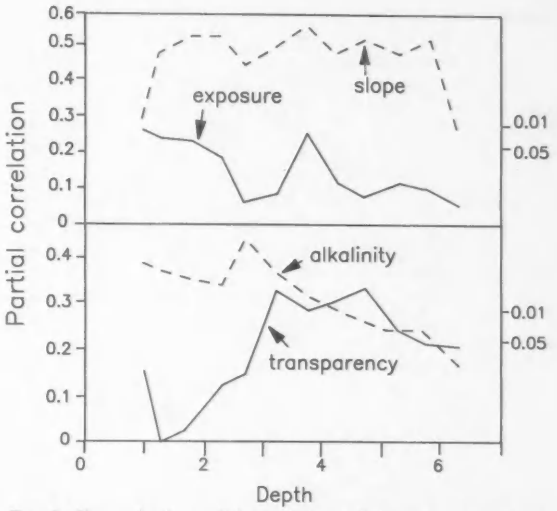

FIG. 5. Change in the partial correlations of slope, exposure, transparency, and alkalinity to macrophyte biomass, with depth. $N > 70$ for all correlations. Numbers on the right side indicate probability levels.

minimum was observed in even the smallest lakes, the increase should reflect not only the attenuation of wave energy with increasing depth but also limitation of the underwater space available for growth in shallow protected sites (Lind and Cottam 1969).

The use of linear regression analysis to model the relationship between biomass and environmental conditions assumes that this relationship reflects a continuous and gradual process. However, the large number of sites without macrophyte growth (Fig. 2) is not easily explained by such a continuous process. Rather, the abundance of bare sediments suggests the existence of threshold conditions that determine whether plant growth can or cannot occur. The steepness of the littoral sets a first limit to plant growth because very steep slopes do not support any plant biomass (Fig. 4). The steepest slope at which plants appear and are able to grow is about 15% (Fig. 4), as calculated by the technique of Breiman et al. (1984) and reported in Duarte and Kalff (1986). Consequently the division of the data into two sets (one set of habitats with slopes steeper than 15% that do not support any plant growth ($N = 302$) and another with gentler slopes ($N = 1098$)) reduced the overall variance by 13% (F-test, $P < 0.0001$). Light limitation defines a second threshold that limits plant growth to depths above the depth of maximum colonization, which is predictable from the Secchi transparency (Eq. 2, Fig. 3). The division of the sites between those above and those below the predicted maximum depth of colonization, which defines the depth where light limitation prevents plant growth, explains a further 9% of the total variance (F-test, $P < 0.0001$).

Further evidence that threshold or noncontinuous models are needed to represent the relationship between submerged macrophyte biomass and site-specific conditions comes from the examination of the biomass–depth profiles (Fig. 2). The profiles suggest that the influence of environmental factors (e.g. alkalinity, littoral slope, wave exposure, and water transparency) on plant biomass differs according to the relative depth of growth. This assertion is further supported by changes in the partial correlation coefficients between biomass and these variables as a function of depth (Fig. 5). The partial correlation coefficients between biomass and littoral slope remain relatively constant at all depths, whereas water transparency shows stronger correlations at greater depths and wave exposure and alkalinity are better correlated to plant biomass at shallower depths (Fig. 5). The greater correlation between macrophyte biomass and alkalinity at shallow depths is consistent with the stronger correlation between water transparency and plant biomass of deep communities and suggests that the latter have light-limited photosynthetic rates, such that they are less influenced by dissolved inorganic carbon (DIC) availability.

Discussion

Relationships between Submerged Macrophyte Biomass and Enviornmental Conditions

The relationship between biomass and alkalinity (Eq. 1, Fig. 1 and 2) adds to the existing evidence pointing to its influence on macrophyte community structure (Moyle 1945; Seddon 1972; Hutchinson 1975; Pip 1979; Hellquist 1980), species richness (Cattling et al. 1986), and productivity (Adams et al. 1978). Further, our results support the conclusion that DIC availability, which is a major component of the alkalinity, is important in the regulation of biomass production by submerged macrophytes in lakes (Spence 1967, 1982; Hutchinson 1975; Wetzel and Grace 1983; Adams 1985; Barko et al. 1986). The relatively abundant evidence for carbon limitation of submerged biomass contrasts with the paucity of similar evidence for phytoplankton (Schindler 1977; but see Talling 1976). The difference may well partially derive from the much slower turnover rate of macrophyte biomass, so that carbon limitation of photosynthetic rates (Adams et al. 1978) would reduce the biomass accumulated throughout the summer, even if the limitation occurs only sporadically.

The vertical extent of the vegetated areas appears to be defined by three threshold phenomena: (1) a deep limit attributable to light limitation (Eq. 2, Fig. 3; Chambers and Kalff 1985; Canfield et al. 1985), (2) a shallow limit probably attributable in our lakes to wave action and/or to spring ice scouring, and (3) a limit to plant growth attributable to the

instability associated with very steep littorals (Fig. 4). The regular change in submerged biomass with depth (i.e. the parabolic shape of the biomass–depth curve) described here (Fig. 2) appears to be an ubiquitous feature of submerged macrophytes in lakes (cf. Spence 1982), resulting from strong vertical changes in the relationship between plant biomass and environmental conditions. The depth changes in the correlation coefficients between plant biomass and wave exposure, water transparency, and alkalinity (Fig. 5) show that macrophyte communities can be differentiated into deep communities (i.e. those growing below the depth of maximum biomass) that appear to be strongly influenced by the underwater irradiance and shallow ones that appear most influenced by physical stress and carbon availability. The development of a biomass maximum in the biomass–depth profile (Fig. 3) corresponds, therefore, to an equilibrium point between light limitation and physical constraints on macrophyte growth.

The change in the partial correlation coefficient between plant biomass and exposure with depth (Fig. 5) is not as great as would be expected from the dissipation of wave energy with increasing depth. On the basis of in situ nutrient fertilization experiments, Duarte and Kalff (1988) concluded that the erosion of fine-grain sediments and their associated nutrients is more important than direct wave action in controlling shallow growing macrophyte communities. Failure to demonstrate strong correlations between exposure and biomass at shallow sites may either reflect an only modest influence of wave action upon shallow growing plants or, as found in one lake (Duarte and Kalff 1988), an influence small compared with the one imposed by nutrient limitations. Alternatively, the measures of wave exposure used were inappropriate measures of wave effects on submerged plants. Submerged plants may well be more influenced by low-frequency extreme wind events than by average conditions, and plant damage by wave action may also differ at different stages of plant growth.

The correlation coefficients between environmental factors and macrophyte biomass are weak (Fig. 5), suggesting considerable unexplained variance in our analysis of site-specific biomass. Since our study did not consider small-scale (i.e. within the macrophyte bed) variability, the large unexplained variance includes the influence of the factors that operate at a scale smaller than considered here. The use of a single estimate of epilimnetic water characteristics instead of using summer means or littoral water samples may further introduce some error in the analysis. Although the use of summer-average water characteristics would have been preferable, we settled for a lower precision to enable sampling of many different sites in many lakes. However, the use of single-date water samples should be a minor problem because the summer variation in epilimnetic characteristics within single lakes is small compared with the broad range in epilimnetic conditions among lakes (see fig. 2 in Forsberg and Heyman 1984). We avoided using littoral water samples because (1) these can lead to spurious correlations to submerged macrophyte biomass in that differences between the littoral and epilimnetic water conditions (e.g. Goulder 1970) are likely to be the result of submerged macrophyte metabolism (Goulder 1969, 1970; Carpenter and Lodge 1986) and (2) littoral data can show wide diurnal oscillations associated with diurnal macrophyte photosynthesis and nocturnal macrophyte respiration (Goulder 1970).

Towards a New Conceptual Framework

Our results support the hypothesis that the relationship between submerged macrophytes and environmental conditions changes with the unit of analysis. Chemical conditions (i.e. DIC) of lake water and lake-average littoral slope are best related to the lake-average biomass whereas the site-specific biomass is related to both site and water characteristics, even though the relationship between site-specific biomass and environmental variables also changes with depth. The results emphasize the complexity of the littoral environment, where environmental gradients associated with depth changes are superimposed on both horizontal variability in littoral morphometry and differences in lake characteristics. The resulting environment is, therefore, much more complex than the relatively homogeneous pelagic environment. As a consequence, the models needed to describe the biomass–environment coupling of littoral organisms are much more complex (e.g. this study; Rasmussen and Kalff 1987) than those used to describe the biomass of pelagic organisms (e.g. Rawson 1955; Sakamoto 1966; Dillon and Rigler 1974; Kalff and Knoechel 1978).

As the ecology of littoral organisms can be studied at different levels (within sites, among sites, among lakes, etc.), the littoral zone biota must be approached from a hierarchial perspective. The regulation of biomass production in submerged macrophytes is best conceptualized as arranged in a nested hierarchy of influence (e.g. latitudinal → water chemistry → littoral morphometry → depth → sediment heterogeneity), each level in the hierarchy comprising different environmental factors and each constraining the possible biomass production further.

Ecologists studying the regulation of submerged biomass at different scales of observation will reach different conclusions. For example, latitudinal related factors (e.g. incoming irradiance) important in the study of worldwide variability in lake-average macrophyte biomass (e.g. Duarte et al. 1986) do not apply at more regional scales (e.g. Canfield and Duarte 1988), which instead suggest DIC as the relevant characteristic (Fig. 1, Eq. 1). Similarly, studies of site-specific biomass within lakes point to the importance of littoral slope, exposure to waves, and sediment characteristics (Duarte and Kalff 1986) whereas studies along single transects point instead to the importance of depth (Spence 1982). There is no reason, therefore, to expect that patterns found at any one scale are transferable to other scales. The recognition of this would reduce the number of unsubstantiated generalizations and extrapolations and minimize irrelevant disagreements about the relative importance of different environmental factors in future research.

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Relative Importance of Phosphorus Supply to Phytoplankton Production: Fish Excretion versus External Loading

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In laboratory tanks with bream (*Abramis brama*), perch (*Perca fluviatilis*), and roach (*Rutilus rutilus*) concentrations of phosphorus and nitrogen increased with time. Phosphorus was mainly released as soluble molybdate-reactive phosphorus (SRP); nitrogen almost exclusively as ammonium. The release increased with the species' tendency to forage on littoral sediments and with a smaller fish size. Bioassays with the test algae *Selenastrum capricornutum* showed that released phosphorus was readily available to algal growth. The total supply of phosphorus to the epilimnion of Lake Gjersjøen was calculated from the external supply from the tributaries and the estimated phosphorus release from total roach biomass. From May to October 1980 phosphorus release from the roach population contributed about the same order of magnitude as the total phosphorus loading from the watershed. During the period with the most serious phosphorus depletion to the phytoplankton (July, August, and September), the phosphorus supply from fish was about double that of the external phosphorus supply, confirming the important role of sediment-feeding fish populations in the eutrophication processes of lakes.

Dans des bassins de laboratoire où se trouvaient des brèmes *Abramis brama*, des perches *Perca fluviatilis* et des gardons *Rutilus rutilus*, les concentrations de phosphore et d'azote ont augmenté en fonction du temps. Le phosphore a été surtout libéré sous forme de phosphore soluble qui réagit au molybdate; l'azote presque exclusivement sous forme d'ammonium. Les quantités libérées étaient proportionnelles à la tendance qu'avait l'espèce de brouter les sédiments littoraux et inversement proportionnelles à la taille du poisson. Des bioessais réalisés avec l'algue *Selenastrum capricornutum* ont montré que le phosphore libéré était facilement disponible aux algues. L'apport total en phosphore à l'épilimnion du lac Gjersjoen a été calculé en fonction de l'apport externe provenant des tributaires et des quantités estimées de phosphore libérées par la biomasse totale des *Rutilus rutilus*. Entre mai et octobre 1980, le phosphore libéré par la population de *Rutilus rutilus* était à peu près du même ordre de grandeur que l'apport total en phosphore provenant du bassin versant. Au cours de la période où l'appauvrissement en phosphore était le plus important pour le phytoplancton (juillet, août et septembre), l'apport en phosphore provenant des poissons était à peu près le double de l'apport externe de phosphore, ce qui confirme le rôle important des populations de poissons limivores dans les processus d'eutrophisation des lacs.

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In recent years the importance of fish to nutrient cycling as well as energy flow in lakes has been emphasized (Hrbaček et al. 1961; Brooks and Dodson 1965; Brooks 1969; Lamarra 1975; Kitchell et al. 1975; Shapiro et al. 1975; Stenson et al. 1976; Andersson et al. 1978; Nakashima and Leggett 1980; Shapiro et al. 1982; McQueen 1986; Benndorf 1987; Benndorf et al. 1988). Lamarra (1975) reported that excretion by bottom-feeding carp (*Cyprinus carpio*) increased phosphorus concentration in lake water and enhanced algal production. In enclosures stocked with dense populations of roach, Andersson et al. (1978) observed blooms of cyanobacteria, in contrast to control enclosures without fish, and described the changes as being similar to eutrophication. However, some authors draw opposing conclusions, e.g. Kitchell et al. (1975) concluded that phosphorus release by planktonic bluegill (*Lepomis macrochirus*) in Lake Wingra (Wisconsin) was not of decisive importance to the phytoplankton compared with the much higher release by smaller organisms such as zooplankton. Nakashima and Leggett (1980) concluded that the maximum quantity of phosphorus excreted by yellow perch (*Perca flavescens*) in Lake Memphremagog was less than 0.33% of the seston demand for this element, while up to 12% of the demand was accounted for by excretion by crustacean zooplankton. In a comment to the conclusions of Nakashima and Leggett (1980); Shapiro and Carlson (1982) stated that "The importance of phosphorus excretion by these fish to the open water phosphorus budget is

best gauged by comparison of the phosphorus excreted with the external loading of the lake."

Kitchell et al. (1975) proposed that fish may stabilize plankton cycles by being a small but continuous source of readily-available phosphorus to algal growth. Fish also influence the amount of phosphorus excreted by zooplankton, by selective predation on large and pigmented species. Thus, fish increase phosphorus turnover rates by causing shifts to smaller zooplankters (Bartell and Kitchell 1978).

The above studies are different in their approach and consider different fish species with different habitat selection. From our studies on roach (*Rutilus rutilus*) in Lake Gjersjøen, a mesotrophic *Oscillatoria*-lake (Faafeng and Nilssen 1981), we know from quantitive echosounding investigations that during summer the roach population exclusively inhabits the epi and upper metalimnion, performing horizontal migrations between the pelagic and the littoral zones during the day. In the littoral zone roach feed on littoral sediments, detritus, and zoobenthos, while in the pelagic zone roach act as planktivores. Consumption of sediments rich in phosphorus by fish with high densities in the photic zone and having a diurnal migration pattern, will increase the relative importance of fish nutrient release to phytoplankton growth. The omnivorous tendency of roach contributes to maintainance of high roach biomass in environments with severe interspecific competition from true zoobenthic-feeding species (Persson 1982; Brabrand 1985), or to reduction of intraspecific competition between different size groups (Persson 1982; Brabrand 1985). From our enclosure experiments (diameter = 1.5 m, depth = 4.0 m) in Gjersjøen during the summer stagnation, we found that even a small roach biomass (less than $2^* 10^{-3}$ g wet wt·L^{-1}) markedly enhanced the concentration of chlorophyll *a*, compared with the control.

Until recently, studies on the effects of fish on phytoplankton production in whole lakes have concentrated on "top-down" effects through grazing via herbivorous zooplankton. The aim of this paper is to elucidate the importance of another fish-phytoplankton interaction, i.e. nutrient supply from fish available to phytoplankton growth. We quantify the contribution of phosphorus from fish in relation to external supply of phosphorus from the tributaries and the supply from the sediments due to high pH.

Study Area

Lake Gjersjøen (area = 270 ha, Z_m = 63 m, Z = 23 m) is situated in southeast Norway, 15 km south of Oslo (Fig. 1). The catchment area (845 ha) consists of Precambrian bedrock, with approx. 15% arable land on marine deposits (Faafeng and Nilssen 1981). During this century the human population increased from about 2000 to more than 25 000, leading to a heavy loading of untreated domestic sewage. Intense blooms of Cyanobacteria (*Anabaena, Aphanizomenon, Gomphosphaeria*, and *Oscillatoria*) developed during the sixties before a tertiary treatment plant came into operation in 1971. Since then spring overturn concentration of total-phosphorus has been close to 18 mg P·m^{-3} and the phytoplankton has been dominated by varieties of *Oscillatoria agardhii*, reaching an annual maximum biomass of 5–10 mg·L^{-1} between the surface and 10 m depth in October. During summer and early autumn *Oscillatoria* shows a characteristic metalimnetic distribution, while during the rest of the year it occupies most epilimnetic depths.

During 1974–81, neither quantitative nor qualitative improvements have been observed in lake phytoplankton, as

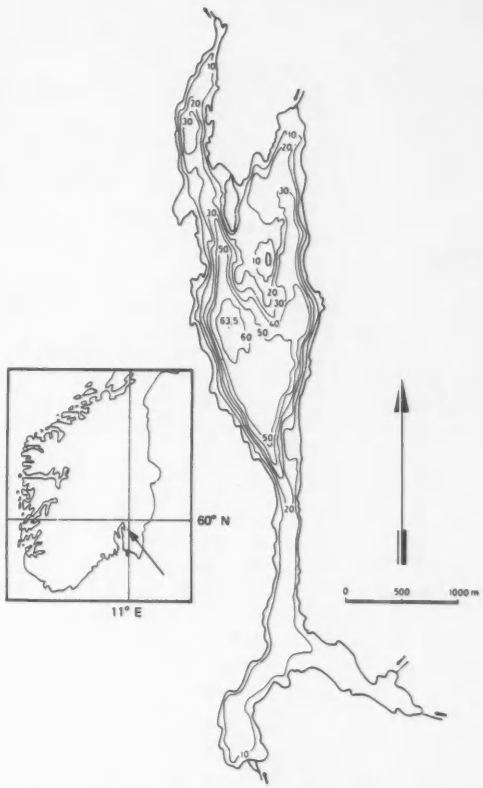

FIG. 1. Lake Gjersjøen, Norway. Depth contours (m).

the lake still exhibits a large biomass of *Oscillatoria agardhii*. According to the phosphorus loading concept, the expected improvement has failed to occur (NORDFORSK 1980), probably on account of biotic processes within the lake ecosystem.

Due to heavy predation from epilimnetic roach, the crustacean fauna is dominated by small forms and species, and the important filter-feeder genus *Daphnia* is dominated by a small hypolimnetic species: *D. longiremis*. The small *Bosmina longirostris* is the most important bosminid.

Pelagic parts of the lake are dominated by roach. The following fish species, in decreasing order of abundance, have a more permanent littoral habitat: perch (*Perca fluviatilis*), pike (*Esox lucius*), bream (*Abramis brama*), rudd (*Scardinius erythrophtalmus*), and eel (*Anguilla anguilla*). Pike–perch (*Stizostedion lucioperca*) was introduced in 1981 in an attempt to increase predation on juvenile stages of roach (published elsewhere).

Materials and Methods

Estimation of total phosphorus release from fish is based upon (1) phosphorus release rates as a function of fish size, (2) a correction to take into account the actual lake temperatures through the growth season and (3) estimation of total fish biomass of different size groups by quantitative echosounding.

Phosphorus Release Rates

Several mathematical expressions have been used to describe the rate of food evacuation in fish species without well defined

stomachs such as cyprinids. An exponential rate function is commonly used, while linear decrease of intestine contents in cyprinids has also been considered (Prejs 1978). To calculate phosphorus release from fish we have measured the increase of nutrient concentrations in tanks containing fish with natural gut contents from the lake, according to Lien (1978). In our study the nutrient release followed an exponential curve during the experimental period as a whole, but continued at a near constant rate after food consumption stopped, enabling calculation of the amount of nutrients lost by the fish (e.g. by defecation and excretion).

Fish were caught by seine nets near the shore of Lake Gjersjøen during daytime (1400–1500 h) in July and September 1980 and July 1983 and in September 1984 from the neighbouring Lake Kolbotnvann. Some fishes were fixed immediately for analysis of gut contents according to the volumetric method described by Ricker (1968). Fish for the experiments were carefully transported to the laboratory and put into 50-L aerated tanks filled with water from the lake (temperature: 17 ± 1°C, 12 hours dark, 12 hours light). For each fish species and size group, three parallels were used. The number of fish in each group varied from five to 20, depending on fish size.

Water samples were taken from each tank for 4 d, and analysed for different fractions of phosphorus, nitrogen, and iron. The release rates and availability of Fe from fish for phytoplankton growth is discussed in a separate paper (Brabrand et al. 1984). The specific release rate of phosphorus and nitrogen were estimated by least squares fit of the increase in phosphorus concentration as a function of time during the linear phase of the experiment. After the linear phase of 18–24 h, the rates decreased to a low, but detectable value until the end of the experiment after 90 h.

For estimation of a whole lake budget, the excretion rates for roach were corrected for temperature according to Persson (1982). He described the rate of gut evacuation versus temperature by the exponential curve:

$$R = 0.032e^{0.115 \cdot T},$$

where R is the rate of gut evacuation (hours) and T is temperature (degrees). In the calculations we used the mean monthly temperatures in the epilimnion from May to October, with maximum temperature in July (20°C) and minimum in October (8°C).

Phosphorus was analysed by standard spectrophotometric methods. Soluable molybdate-reactive phosphorus (SRP) was determined by the molybdate-method on prefiltered (Whatman GF/C) samples (Strickland and Parsons 1968), whereas total-phosphorus was determined as SRP after digestion with potassium persulphate. NH_4-N was determined by reaction with hypochlorite and phenol to give indophenol (Koroleff 1970). Total-nitrogen was determined as NH_4-N after oxidation with UV-radiation at low pH in the presence of H_2O_2.

Nutrient Availability

Availability of released nutrients from fish to algal growth was determined with the test algae *Selenastrum capricornutum* Printz in the laboratory (Källqvist 1975). Water samples from the tanks were filtered through a Whatman GF/C filter and phosphorus, nitrogen, and iron were added separately and in combination in three replicates in order to identify the limiting nutrient(s) for algal growth. Before the tests were carried out, *Selenastrum* was grown on phosphorus-limited medium to prevent storage of phosphorus in the cells. The samples were incubated with 10^6 cells$^{-1} \cdot$L^{-1} at 20°C on a shaking-table at constant light of 6000 lux. Specific growth rate was estimated by least squares fit of log-transformed cell number as a function of time in the exponential growth phase.

Pelagic Fish Biomass

Density of fish and the fish size distribution in the pelagic zone of Lake Gjersjøen was investigated along representative transects with a quantitative echosounder (SIMRAD EY-M). A description of the echosounder is given by Lindem (1979). The working frequency of the system is 70 kHz, and the duration of the transmitted pulse is 0.6 ms, giving a depth resolution of about 0.5 m. The echosignals are scaled down from 70 to 10 kHz at the calibrated signal output, making it possible to record the analog signal on a high fidelity tape recorder, Nakamichi 550. All data have been recorded with a $40 \cdot \log R$ time varied gain control (TVG), applied to the preamplifier. Echosignals were recorded on magnetic tape and analyzed on a microcomputer according to the method described by Craig and Forbes (1969) and modified by Lindem (1979).

On each occasion the echosounder was operated during both night and day to obtain information of diurnal distribution of the fish populations. During the day, the fish were observed in schools, contributing to spatial heterogenity of the fish population. At night the schools dispersed and single fish were distributed more evenly along the recorded transects. The even distribution at night seems also to occur in littoral areas, as catches of roach per unit effort by gill nets is not significantly different. During all the echosounding recordings, the fish always showed an even horizontal distribution in the pelagic zone. During spring and summer the fish were often located close to the water surface, making it impossible to record them by the echosounder, leading to serious underestimation of fish biomass. However, during autumn the fish were more associated with the upper metalimnion, enabling a more precise estimation of fish biomass. The calculations of total phosphorus release are therefore based on echosounding recordings during September 1980.

The echosounding system is based on the fact that mean echo intensity, or target strength (TS), increases with increased fish size. Reflected echosignals from the depth interval 2–10 m below the transducer were analysed. Single echosignals were sorted to target strength intervals of 2 dB, reflecting different size groups of roach (see below) and the number in each interval counted.

Parallel to the echosounding recordings, fishing was carried out with seine nets (mesh size in the bag: 5 mm) and with floating gill nets (mesh size: 10, 19.5, and 21.5 mm). All pelagic catches were dominated by roach of size group approximately 60–95 mm, age group 2+. It has to be stressed that only the pelagic part of the roach population was recorded by the echosounding.

As roach was by far the most abundant fish species (>90% by numbers) in all catches in the pelagic zone with plankton nets, floating gill nets, surface seine and trawl, we conclude that the echosignals reflect the pelagic part of the roach population.

Statistics of Fish Biomass and Phosphorus Release

The methods for calculation of pelagic fish biomass from recorded echosignals and further estimation of statistical errors

are outlined in detail by Bjerkeng et al. (1990). A condensed explanation of the calculations is given below.

The linear relationship between target strength (TS) and fish length (L) is given by Lindem and Sandlund (1984):

$$(1)\quad TS = 20 \cdot \log_{10}(L) - 68$$

A study of data from Gjersjøen and another roach-dominated lake gave no basis for choosing a different relationship (see Bjerkeng et al. 1989).

By using different data sets, available from the literature and the present study, for weight as a function of length, and for phosphorus release as a function of weight, two log-linear relationships have been established (equation (3) and (4)).

The set of equations used may be written:

$$(2)\quad \ln L = a + b \cdot (TS - \tau)$$

$$(3)\quad \ln W = c + d \cdot (\ln L - \lambda)$$

$$(4)\quad \ln R_{22} = g + h \cdot (\ln R - \omega)$$

where

TS = target strength of echo signal (dB),
L = fish length (cm),
W = fish weight (g),
R_{22} = phosphorus release rate (μg SRP·h^{-1}·g fish^{-1} at 22°C),
τ = mean TS in the data set used in estimating equation (2),
λ = mean ln in the data set used in estimating equation (3),
ω = mean ln W in the data set used in estimating equation (4)
a,b,c,d,g,h = coefficients estimated from data.

When the equations are written this way, all coefficient estimates have independent errors if ordinary linear regression assumptions are valid.

The final estimates for the parameters in equation (2) which are used in the calculations are:

$$a = 2.514 \qquad b = 0.112 \qquad \tau = -46.5$$

The coefficient in equation (3) was estimated from data obtained by trawl catches in lake Gjersjøen, and fitted well the results given by Papageorgiou (1979):

$$c = 1.15 \qquad d = 3.09 \qquad \lambda = 2.012$$

The coefficients in equation (4) was estimated from data given by Lamarra (1975) in combination with data obtained in experiments as a part of the present study. The resulting values for the coefficients of equation (4) is:

$$h = 0.53 \qquad g = 4.18 \qquad \omega = 2.06$$

Equation (4) can then be written as:

$$(4a)\quad R_{22} = 22\, W^{0.53}$$

This relation is used for fish down to a weight of 2.8 g. For smaller fish, which in general belong to age class 0^+, a maximum value of 13.5 μg P·h^{-1}·g^{-1} fish at 22°C is used instead, according to the observed release rates. This leads to the relation:

$$(4b)\quad R_{22} = 13.5\, W$$

The two equations (4a) and (4b) intersect at $W = 2.8$ g.

The phosphorus release rate as a function of temperature is given by the equation:

$$(5)\quad \ln R = \ln R_{22} + p \cdot (T - 22°C),$$

where

T = water temperature (°C).
R = phosphorus release (μg SRP·h^{-1}·g fish^{-1} at temperature T).
p = coefficient estimated from data.

Given a set of fish density values $D(i)$ for target strength classes $TS(i)$ ($i = 1,..n$), the total phosphorus release (F) for a lake area A can be estimated by:

$$(6)\quad F = A \cdot \sum_{i=1}^{n} \left(\sum_{k=1}^{D(i)} R(i,k) \right),$$

where

$R(i,k)$ = respiration for a single fish given as a stochastic variable.

Expectation value and variance of F can be calculated for measured $D(i)$ if the statistical properties of $D(i)$ and $R(i,k)$ are known.

Error estimates for F in equation (6) are based on the following error sources:

1) Statistical errors in estimated model parameters a,b,c,d,g,h,p.
2) Error due to discretisation of TS scale into 2 dB classes. An age class of fish is often found within one or two TS intervals, and the discretisation therefore means that the peak value cannot be precisely determined.
3) Stochastic variations for single fish around expectation values, due to different orientation of single fish.
4) Statistical errors in the calculated fish densities.

Expectation values and variance of F are mainly expressed as a function of expectation and variance of each term in equation (6) with equation (1) through (5) inserted by means of 1 standard order analysis of error.

In order to estimate the expectation value of the different terms, we apply the general result that a function $y = e^x$ where x is normally distributed, has an expectation value $E(y)$ given by the expectation value $E(x)$ and variance $V(x)$ as:

When: $y = e^x$

Then: $E(y) = e^{E(x) + V(x)/2}$

$$V(F) = \mathrm{E}(y)^2 \cdot (e^{V(x)} - 1).$$

F and $V(F)$ were calculated by inserting the estimates of the variances into the residual error.

External Phosphorus Loading

The phosphorus input f for each observation date is calculated as the sum of the four main tributaries running into lake Gjersjøen, and multiplied by 1.25 to correct for the fact that these drain about 80% of the total catchment area.

Monthly means of phosphorus input are calculated as arithmetic means of the observed transport values within each month and, according to usual practice, corrected for the difference between mean water flux on observation dates and daily mean water flux, based on continuous measurements.
The formula used is:

$$(7)\quad F = E_1(f) \cdot \frac{E_2(q)}{E_1(g)} \cdot 1.25 \cdot T_m$$

where

$$E_1(f) = \frac{1}{N}\sum_{i=1}^{N}(f_i) = \text{mean of observed transport values,}$$

$$E_1(q) = \frac{1}{N}\sum_{i=1}^{N}(q_i) = \text{mean of water flux for observations of phosphorus concentrations,}$$

$$E_2(q) = \frac{1}{M}\sum_{k=1}^{N}(q_k) = \text{daily mean water flux based on measured values,}$$

and where

F = total monthly phosphorus input (kg/mo),
f_i = single observation of phosphorus input to Lake Gjersjøen, as sum of concentration times water flux in the four streams,
q_i = sum of water flux in the four streams (kg/d),
i = index of phosphorus input value (1,...,N),
k = index of daily water flux mean value (1,...,M),
N = number of phosphorus input values per month,
M = number of daily water flux values,
T_m = approximate number of days in month (= 30.5)

The stochastic error of each monthly mean value could be estimated by ordinary standard deviation for the observations within the month, but since the variations to a large extent reflects real changes in time, and not only stochastic error, this would obviously exaggerate the error. Instead, error estimates are based on analysing the fluctuations over time in data spanning the 14 yr from 1971 to 1984. After log transforming the f data series the deviations of a single f value from a straight line between two surrounding values in time are analysed. As would be expected, it is found that the mean square of such deviations increases with the time interval between the two surrounding observations, and is largest when the midpoint is located near the middle of the time interval.

For such midpoints the mean square deviation in log ± of phosphorus input (f) can be expressed by:

$$(8)\quad \text{var}(\log(f)) = 0.0056 \cdot T^{0.766},$$

where

T = time interval in days between surrounding observations.

This is then applied as an estimate of how well one observation represents a surrounding time interval of length T, using a constant T for all observations in a month.

pH-Dependent Phosphorus Release

Release of phosphorus from epilimnetic sediments in contact with water at different pH was measured on intact sediment cores. Although the sediment in the neighbouring Lake Årungen released considerable amounts of SRP at high pH (Sanni 1986), similar experiments on epilimnetic sediments from Lake Gjersjøen showed that they were of negligible importance for the phosphorus budget of this lake.

Results

Gut Contents

Gut contents of roach from Lake Gjersjøen were dominated by littoral sediments; more than 70% in both the small and the larger roach was sediment, although detritus and benthic algae were also present. Bream fed similar to roach, but zoobenthos was more strongly selected. In perch guts, copepods and larval chironomids dominated. The amounts of iron released by the different fish species followed the consumption of sediments, as the sediments themselves had an iron content of 0.6% by dry weight, and hence confirmed the observations of gut contents.

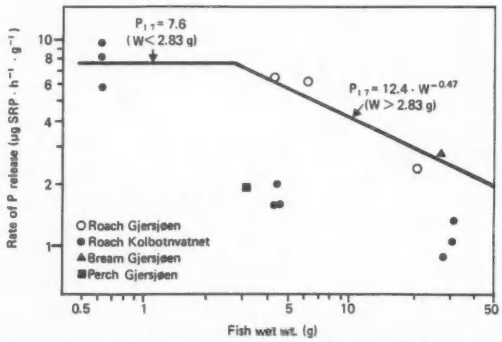

FIG. 2. Relationship between phosphorus release rates (SRP) at 17°C (P_{17}) and roach wet weight (W) of sediment feeding roach (○) from Lake Gjersjøen and zoobenthivorous roach (●) from Lake Kolbotnvann. Phosphorus release rates from sediment feeding bream (▲) and perch (■) feeding on animal food items from Lake Gjersjøen are marked, showing the influence of food intake.

In the gut contents of roach from Lake Kolbotnvann, zooplankton was the dominant food item in the age group 0+, while zoobenthos and detritus were observed in the larger size groups. No sediments were observed in the gut contents of roach from this lake, which was also confirmed by the lack of any detectable release of iron.

Nutrient Release Rates

Phosphorus from all the three fish species and all size groups of roach was largely observed as soluble molybdate-reactive phosphorus (SRP) in the water, accounting for up to 100% of total-phosphorus from roach, although usually 85–95%. Thus, most of the phosphorus was dissolved in the epilimnion rather than precipitated as fecal pellets. The major part of the nitrogen was present as ammonium.

Sediment-feeding roach from Lake Gjersjøen released phosphorus at a higher rate than roach from Lake Kolbotnvann (Fig. 2), because the latter did not consume sediments. In Lake Gjersjøen the SRP release rate at 17°C was calculated to $P_{17} = 12.4 \times W^{-0.47}$ for roach larger than 2.83 g wet weight (W). As the 0+ age group in general and also in Lake Gjersjøen fed mostly on zooplankton, phosphorus release of this age group in Lake Gjersjøen was similar to that of Lake Kolbotnvann.

Phosphorus release rate from small perch consuming animal food items was less than one-third of the value from small sediment feeding roach from Lake Gjersjøen and close to values of nonsediment feeding roach from Lake Kolbotnvann. Bream feeding on sediments on the other hand showed values close to sediment feeding roach.

The nitrogen–phosphorus ratio released from roach was about 12 (by weight), indicating near ideal composition for phytoplankton growth.

Availability of Nutrients

In lake water with no additions and with addition of nitrogen only, growth rates of *Selenastrum capricornutum* were near zero

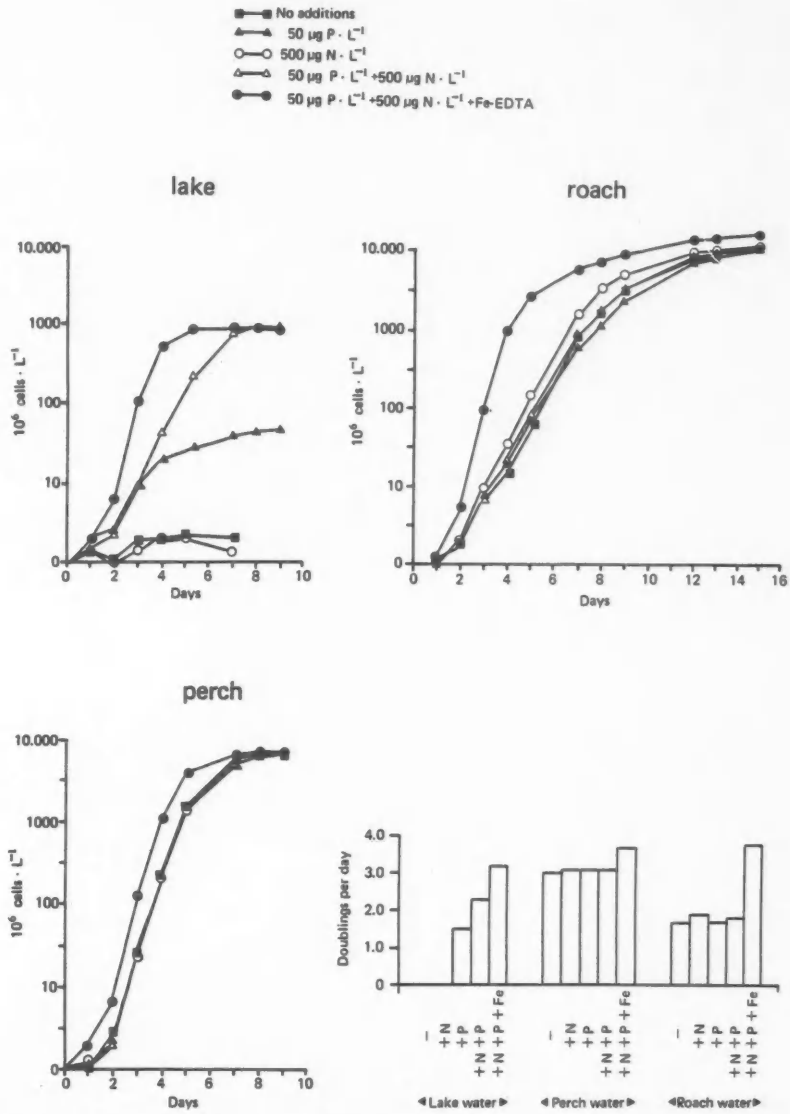

FIG. 3. Growth curves of *Selenastrum capricornutum* Prinz in lake water and water exposed to excretion and gut evacuation products from roach and perch with and without additions of phosphorus, nitrogen, and iron-EDTA. Specific growth rates (doublings·d^{-1}) in lake water and water from roach and perch increased after addition of iron-EDTA.

(Fig. 3). Addition of phosphorus increased growth rate and the total cell yield, while addition of phosphorus and nitrogen in combination increased total cell yield 20 times compared with phosphorus alone. Specific growth rate, but not total yield, was increased by addition of chelated iron. In the tests of water from the tanks with perch and roach no increase in growth rate and cell yield was observed after additions of phosphorus and nitrogen. The reason for suboptimal growth rate in the water exposed to roach without additions of chelated iron (Fig. 3) is discussed elsewhere (Brabrand et al. 1984).

Epilimnetic Phosphorus Input

Fish contributed considerable proportion of total phosphorus input to Lake Gjersjøen during the ice-free period (Fig. 4). The budget is based on an estimated roach biomass of 300 kg·ha^{-1}. In total, phosphorus released by roach represented approximately 35% of the two "external" sources to the epilimnion from May to October, based on data from 1980. pH-dependent phosphorus release from sediments was found to be negligible in this lake. On an annual basis the supply from the watershed was estimated to 10.7 kg·ha^{-1}·yr^{-1}, while from fish it was 4.4

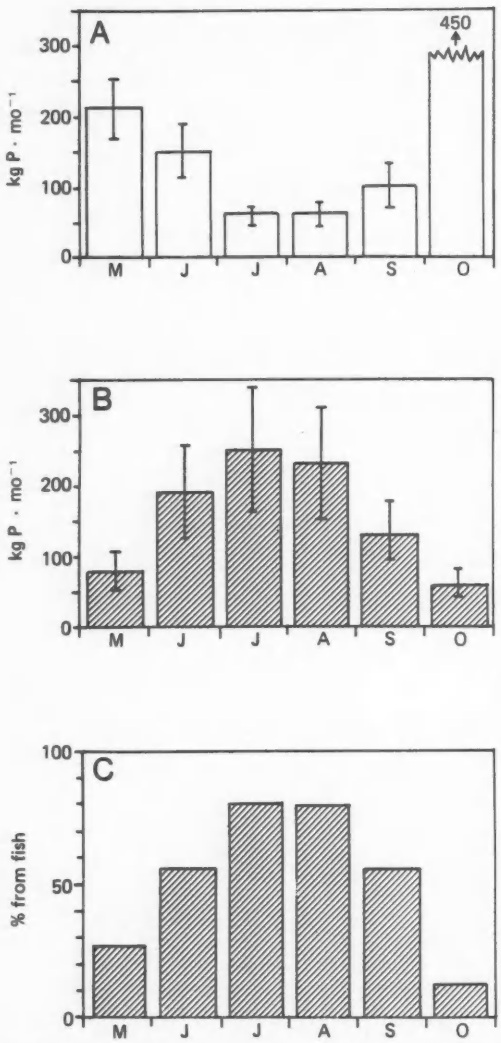

FIG. 4. Total phosphorus supply ($kg \cdot mo^{-1}$) to Lake Gjersjøen. Standard deviation is shown. (A) Estimated external loading of phosphorus from the tributaries. (B) Total release of phosphorus (SRP) from roach biomass in Lake Gjersjøen. (C) Percentage contribution of phosphorus from fish to Lake Gjersjøen.

$kg \cdot ha^{-1} \cdot yr^{-1}$. However, fish phosphorus release was evidently of special importance during July and August, when fish contributed about 80%, or 0.9 $kg \cdot ha^{-1} \cdot mo^{-1}$, while the watershed contributed 0.2 $kg \cdot ha^{-1} \cdot mo^{-1}$. The relative standard deviation for phosphorus release from fish was about 35% in all months, for the watershed 20–30%.

The general input pattern of total phosphorus from fish reflects the temperature through the season as the main factor to phosphorus release by a given fish biomass. The contribution from the tributaries shows an inverse curve due to low precipitation and hence low water flow in the tributaries during summer.

Discussion

The rates of phosphorus release is obviously influenced by the food consumed by the fish, as sediment-feeding roach showed significantly higher phosphorus release rates than benthivorous roach and planktivorous perch. When feeding on loose, littoral sediments, phosphorus is released as SRP from ironcomplexes, probably due to anaerobic conditions in the gut. In contrast, when fish feed on animal food components or plants, the detritus food chain is primarily stimulated. In this case the sedimentation of fecal pellets is more dominant, and further microbial activity is needed before phosphorus is available for algal growth. However, in both cases we found SRP to be the main phosphorus component. This is in contrast to the experiments of Lamarra (1975), in which approximately 50% of total phosphorus was SRP, or to the results of Sternik (1983) where carp fed on high-protein pellets giving excretion products consisting predominantly of particulate phosphorus. To obtain a relative constant energy intake, food intake by the fish is dependent on the energy content of the diet. In roach the consumption rate is considerably lower when fed on high-energy food, compared with low-energy food as plants (Hofer et al. 1982, 1985). The shift to increased intake of low-energy food such as plants, detritus, and sediments will therefore increase phosphorus regeneration by roach.

Taking into account the differing temperature conditions, the release rates of SRP from zoobenthivorous roach are in accordance with the results of Lamarra (1975), but neither rates of sediment feeding nor zoobenthivorous roach are statistically significantly different from those of the carp. However, rates of phosphorus release seem more dependent on food quality than on fish species, notably the amount of sediment intake. In total phosphorus budgets for fish populations, a more precise description of phosphorus release versus different types of food consumed therefore seems necessary.

The availability of phosphorus in August and September is believed to be of decisive importance to the development of a continuing cyanobacteria bloom during the early autumn. As this is usually a relatively dry season, the tributaries supply only small amounts of nutrients to the lake. Therefore, any other sources will be of greater relative importance at this time of the year. From 1974 to 1982 the spring diatom bloom was always followed by a slow, but continuous increase of *Oscillatoria* throughout the growing season until October. This contrasts with the expected drop in chlorophyll *a* and algal biomass after the spring peak. Phosphorus depletion usually follows the sedimentation of diatoms in early summer. The phosphorus release from fish will increase at this time in the growth season due to higher water temperature and increased fish metabolism. This will maintain phosphorus supply to the lake epilimnion at an almost constant rate during the summer, when external loading from the tributaries are low and the demand of phosphorus by phytoplankton is high. The distribution of roach restricted to the phototrophic stratum will obviously maximize the effects of fish. The ability of intracellular storage of phosphorus, low but steady growth rate even at low nutrient concentrations and low light saturation values of cyanobacteria favour its growth and annual dominance in lakes with epilimnetic phosphorus supply from fish. The experiments by Reinertsen et al. (1986), concerning the patchy release of phosphorus by fish and the more homogenous release by zooplankton, favor the hypothesis that phosphorus supply from fish increase the dominance of cyanobacteria.

Recycling of phosphorus through zooplankton in the epilimnion in September 1980 was calculated to about 8 mg $P \cdot m^{-3} \cdot d^{-1}$, according to quantitative samples and the equations of Peters (1975). Fish excretion rates were less than one-tenth of those from zooplankton, which compare with earlier reports (Nakashima and Leggett 1980). Likewise, recycling of phosphorus by bacteria is presumably orders of magnitude greater than by fish. However, it is necessary to bear in mind that zooplankton as well as bacteria and protozoa, do not add "new" phosphorus to the epilimnion, but recycle already existing particulate phosphorus in the water, whereas sediment-feeding fish redistribute nutrients bound to the sediments, which otherwise are not available for algal growth. The relative importance of phosphorus input from fish to Lake Gjersjøen is in accordance with Shapiro et al. (1982) who judged the loading of phosphorus from benthivorous fish in Lake Marion on an annual basis to be of the same order of magnitude as the external loading.

This is in contrast to the approach of Nakashima and Leggett (1980) who compared phosphorus supply from fish and zooplankton with the phosphorus demand of seston in Lake Memphremagog, Canada. In addition we feel that population estimates based on recapturing of marked fish by gill nets can easily underestimate small fish, which have the highest rate of phosphorus release. Using the data given by Nakashima and Leggett (1980) a mean pelagic perch density of approximately 1050 individuals$\cdot ha^{-1}$ is calculated, including age group 2+ and older. This is 5% of the estimated roach density in Lake Gjersjøen determined by echosounding. The total phosphorus release rates of perch in Lake Memphremagog appear to be of the same order of magnitude as the release rates of roach in our experiments, but consumption restricted to animal food items does not add "new" phosphorus to the epilimnion.

The estimates in Fig. 4 are based on several assumptions; that our echograms are representative for the pelagic part of the roach population, that the roach regularly move to the littoral zone to forage on the sediments and that they have a continuous 24 h food ingestion. Hofer et al. (1982) found no significant difference between nighttime and daytime values for gut passage under laboratory conditions, and assumed a constant diel feeding pattern. In our experiments the release of phosphorus was not influenced by the day/night rhythm. Under natural conditions the diurnal feeding rhythm in roach seems to be flexible, but according to Prejs (1978) it decreases during periods of total darkness. This behaviour seems to be less distinct in young roach, or even opposite as observed by Bohl (1980).

The movement of the fish population is confirmed by our regular observations that the guts of roach caught in the pelagic contain a large proportion of sediment both during day and night. On the other hand, a change in evacuation rate due to "stress" during the experiment may occur. In a study by Persson (1982) roach needed 24 h starvation at 16.4°C to empty their intestines, which confirmed Bohl's earlier results (1980). This period is in accordance with the linear phase of our study. However, laboratory conditions seem to decrease the rate of gut evacuation, and Prejs (1978) assumes roach of even 19–24 cm empty their guts in 5–6 h at summer temperatures. According to Hofer et al. (1982) the gut passage time was independent of fish size for adult roach (12–18 cm), and was about 4.5 h at 20°C. The commonly reported low values for gut passage time probably refer to artificially low consumption rates under laboratory conditions. Thus, the experimental conditions in our study probably lead to an underestimation of the rate of phosphorus released by roach.

The statistical error in the results of total phosphorus release by the roach population is mainly caused by three sources:

The dominant source of error is the statistical error in the estimated coefficient g in equation (4), alone accounting for 35–80% of the total variance. Since this coefficient is estimated from three experimental points only it seems probable that more specific experimental data on release rates for fish from Gjersjøen might considerably reduce this error.

The second most important factor is the estimated fish density, accounting for 5–50% of the total variance. This error estimate is made in a somewhat speculative manner, and chosen as the maximum indicated by available data. Thus the estimated error may be too large. By making repeated echosoundings and calculating the statistical error in $D(i)$ empirically, one should be able to reduce this error to a small fraction of that indicated above.

Together these two error sources account for about 85% of total variance in all cases. Thus, if the standard deviation of these errors could be reduced by 50%, the relative error in the estimated phosphorus release rates would be reduced from 35–50% to 20–30%.

The third main source of error is the uncertainty in length peak value for fish in a given TS interval, accounting for about 10% of the total variance. This error is part of the echosounding method, and is more difficult to reduce.

The estimated pelagic fish biomass varied considerably throughout the season. For the lowest estimates, only the small fish from age class 0+ were observed in the pelagic zone and therefore detectable by the echosounder. If we assume that total fish biomass through the season is approximately constant, and that fish behaviour influenced the detectability of fish, the largest estimate can be used to estimate phosphorus release from fish. The largest roach biomass estimated by echosounding was 300 kg$\cdot ha^{-1}$, and the total phosphorus contribution from roach was based on the assumption that this biomass is representative for the lake as a whole. The largest roach biomass was observed in September 1980, after summer production of roach but before winter mortality. The estimated roach biomass is comparable with lakes of the same trophic status. Roach biomass in the more shallow and neighbouring Lake Årungen was estimated by the Petersen mark and recapture method to vary between approximately 150 to 700 kg$\cdot ha^{-1}$ in the period 1979–83 (Borgstrøm 1984). The estimated roach biomass in Lake Gjersjøen is probably too low due to underestimation of the littoral part of the roach population. However, it is important to note that the littoral part of the fish population also contributes to phosphorus recycling.

The large variation observed in summer chlorophyll concentrations in lakes with equal spring overturn concentrations of phosphorus is generally explained by external phosphorus-loading, lake morphometry, zooplankton grazing, etc., but internal phosphorus-sources is documented to play an important role. As shown earlier considerable amounts of other nutrients such as iron (Brabrand et al. 1984), and also nitrogen may be reactivated by fish. This confirms the suggestion of Andersson et al. (1978) and Shapiro et al. (1982) that management of the fish populations might be an efficient means of controlling phytoplankton abundance. As roach and several other cyprinids increase markedly during eutrophication, the activity of these and other benthivorous fish species may be one of the factors responsible for the slow recovery of such lakes.

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Longitudinal Structure of an Agricultural Prairie River System and its Relationship to Current Stream Ecosystem Theory

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The largescale structure of an agriculturally developed prairie river system in central Illinois was examined and compared with predictions from current stream ecosystem theory. High rates of primary productivity (>15 g carbon·m^{-2}·d^{-1}) were characteristic of the watershed, although longitudinal patterns in riparian vegetation, stream temperature, and primary productivity were inverted relative to typical streams in forested uplands. Empirical models of gross primary production and community respiration were developed. Light availability, mediated by both channel shading and turbidity, appeared to be the principal factor limiting primary productivity. Both nitrate and orthophosphorus were found in high concentrations throughout the watershed. Largescale patterns in nutrient availability suggest that landuse patterns, and particularly urbanization, strongly affected spatial and temporal distributions of both nutrients. Differences between prairie river systems and "prototype" structures envisioned by the River Continuum Concept (RCC) derive from the descriptive nature of the RCC, and its inability to incorporate nonstandard distributions of key driving variables. The use of empirical modelling in stream ecosystem studies is discussed.

La structure à grande échelle d'un réseau hydrographique de prairie, à développement de type agricole, du centre de l'Illinois a été examinée et comparée aux prédictions obtenues selon la théorie actuelle des écosystèmes lotiques. Un taux élevé de production primaire (>15 g de carbone·m^{-2}·d^{-1}) caractérisait le réseau, mais les patrons longitudinaux de la végétation riveraine, de la température des cours d'eau et de la productivité primaire étaient inversés par rapport aux cours d'eau typiques des hautes terres boisées. Des modèles empiriques de la production primaire brute et de la respiration de la communauté vivante ont été élaborés. La disponibilité de la lumière, influencée à la fois par l'ombrage du lit et par la turbidité, semblait être le facteur principal limitant la productivité primaire. On a trouvé en fortes concentrations du nitrate et de l'orthophosphate dans tout le bassin. La configuration à grande échelle de la disponibilité des nutriants semble indiquer que les schémas d'utilisation des terres, et particulièrement l'urbanisation, influent fortement sur la répartition spatiotemporelle de ces deux nutriants. Les différences entre les systèmes hydrographiques de prairie et les structures « prototypes » prévues par le concept de continuum lotique (RCC) proviennent de la nature descriptive du RCC et de son inaptitude à intéger des distributions non standard des variables clés. Nous analysons l'emploi de la modélisation empirique dans les travaux sur les écosystèmes lotiques.

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The influence of streamside vegetation on the structure and function of stream ecosystems has received growing attention over the past decade (Cummins 1973, 1974; Cummins et al. 1984; Hynes 1975; Vannote et al. 1980). Recently, patterns in riparian vegetation have been proposed as a primary organizing factor in theoretical constructs arising out of the river continuum paradigm (Cummins et al. 1984; Minshall et al. 1985). It is surprising, then, that grasslands in general, and the agriculturally developed prairie watersheds of midwestern North America in particular, have received so little attention. Grasslands and agricultural fields cover roughly 42% of the earth's land surface (Smith 1980), and watersheds draining these areas provide an almost ideal inversion of the typical longitudinal structure of riparian vegetation described in the continuum literature (Vannote et al. 1980). Prairie streams, like those of desert regions (Busch and Fisher 1981; Grimm et al. 1981; Cushing and Wolf 1984; Grimm and Fisher 1986) are primarily open in their upper reaches, with riparian canopies developing downstream. However, unlike true desert systems, prairie rivers have perennial flows and are hydrologically a more useful contrast to rivers in forested uplands. For this reason, prairie watersheds provide an important natural laboratory in which theories about the impact of patterns in riparian vegetation (and other large-scale watershed characteristics) on stream ecosystems can be empirically tested and refined.

Previous investigations of prairie river systems have demonstrated that upstream sites are frequently, but not necessarily, autotrophic. Duffer and Dorris (1966) reported gross primary

production rates of up to 48 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in Oklahoma, but found only one of three sites consistently had a ratio of gross primary production to whole community respiration (P:R) greater than 1. Gross primary productivity reached a maximum of 32 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in an agricultural watershed in Kansas and mean P:R ratios exceeded 1 in half the sites examined (Prophet and Ransom 1974). More recently, Gelroth and Marzolf (1978) found a P:R ratio >2 in a small prairie stream. High nutrient levels (N and P) are also common in prairie watersheds, a fact often directly attributed to agricultural activities (Prophet and Ransom 1974; Kilkus et al. 1975; Omernick 1977).

In this paper, we summarize the results of a 2-yr investigation of spatial and temporal patterns in community metabolism in a typical prairie watershed in east-central Illinois. Land-use characteristics, gross primary productivity (P), whole community respiration (R), nutrient concentrations (soluble reactive phosphorus and nitrate-N) and physical control variables (percent shade, temperature, and turbidity) were examined with respect to their longitudinal structure in this heavily agricultural watershed. We argue that the longitudinal distribution of photosynthesis principally reflects downstream patterns in light limitation and not nutrient availability in this river system. Due to the inverted patterning of riparian shading in these rivers, longitudinal profiles of primary productivity deviate strongly from that predicted by current theory. The utility of the river continuum concept (RCC) (Vannote et al. 1980) in understanding the structure and function of prairie watersheds is discussed.

Methods

Study Area

This study was conducted in two adjacent branches of the Vermilion River (tributary to Wabash) in east-central Illinois, USA (see inset map, Fig. 1). Prior to conversion to agriculture, both branches drained primarily seasonally innundated tallgrass prairie and marshlands (Ames 1970; Barker et al. 1965). The Vermilion has a long history of scientific investigation because of its close proximity to the University of Illinois, and the Illinois Natural History Survey (Champaign-Urbana, Illinois) and detailed descriptions of geography, soils, climate, landuse, and aquatic fauna can be found elsewhere (Thompson and Hunt 1930; Larimore and Smith 1963; Wickham 1979; Wiley et al. 1987; Osborne and Wiley 1988; Munn et al. 1989). The watersheds of the Salt Fork and Middle Fork are adjacent and encompass approximately 1204 km^2 and 1109 km^2, respectively. The upper regions of both watersheds were channelized from 1890 to 1920 to facilitate drainage. No significant new channelization has occurred within the study area during the past 60 yr. The principal effect of early channelization was to increase the total length of the drainage network by extending upstream channels into prairie wetlands.

Substrate composition in both rivers was similar. Substrate in the upper portions consists of coarse sands, reflecting the low slope of these areas. Corresponding with increases in slope, lower reaches of both rivers are dominated by small cobble and rubble in riffle areas and by sand and silt in pools. Thirty-two sampling locations were established in the two watersheds (Fig. 1a) and were sampled periodically over 2 yr for physicochemical characteristics and rates of community metabolism.

Riparian Structure and Land Use

Watershed boundaries for each sampling station were digitized from 7.5-min (1:24 000) United States Geological Survey topographic maps. Land-use/cover patterns were determined for each station watershed by interpreting false-colored infrared National High Altitude aerial photographs (1:20 000 scale; film exposure April 1981 and 1983; U.S. Department of Interior, EROS Data Center, Sioux Falls, South Dakota). All data were interpreted on to mylar sheets to minimize distortion, digitized, and analyzed using ARC/INFO (Environmental Systems Research Institute), a geographic information system running on a PRIME 750 minicomputer. Six land-use classifications were employed in the study: (a) urban and developed lands, (b) agriculture land, (c) forested land, (d) water (lakes and streams), (e) wetlands, and (f) barren lands (e.g. mining areas). Land use was characterized for each sampling station as the proportional contribution of each category to the total drainage area.

Water Chemistry

Water chemistry data were collected at approximately 2-wk intervals from December 1983 to December 1985 providing representative water chemistry concentrations during the study period. Nitrate-N, nitrite-N, ammonia-N, turbidity, minimum and maximum biweekly temperature, specific conductance, pH, and soluble reactive phosphorus (SRP) were measured, although only nitrate and SRP data are analysed here.

Water temperatures were measured using maximum–minimum thermometers anchored in the stream. Duplicate water samples were collected (one acidified) and returned to the laboratory for analysis. Nitrate-N in acid preserved samples was measured spectrophotometrically using cadmium reduction or (for high range measurements) cadmium reduction substituting gentisic acid for 1-naphthylamine. Nitrite-N was determined using the diazotization procedure incorporating chromotropic and sulfanilic acids as indicators. Ammonia-N was measured using the Nessler method. Soluble reactive phosphorus was determined using a modification of the molybdenum blue procedure (Hach Chemical Co. 1982).

Quality control tests were conducted to assure the accuracy of the above procedures and the precision of the laboratory analysts. Voluette ampule standards with known concentrations of nitrates, ammonia, and reactive phosphorus were supplied by the U.S. Environmental Protection Agency. Two replicates of each test were performed on voluettes with varying concentrations of each nutrient. Voluette concentrations were unknown to laboratory analysts prior to and during testing. All results fell within the 90% confidence interval, and all SRP and ammonia-N results were within the 95% confidence interval. Periodic checks of the accuracy of spectrophotometric determinations were made throughout the study by performing parallel analyses with a technicon auto-analyzer.

Community Metabolism

Community photosynthetic and respiration rates were estimated using a single-station open-channel regression technique (Owens 1974; Kosinski 1984) based on Odum's original single-station method (Odum 1956). Diel records of oxygen concentration and temperature (and in some cases, light) were obtained from selected stations using automated data logging units ($n = 191$) or manual monitoring ($n = 97$). In both cases, saturation-calibrated YSI Model 57 oxygen meters were employed. Meter drift during automated collection was generally <1 ppm and for each estimate was distributed evenly throughout the data set. The mean night-time respiration rate and reaeration coef-

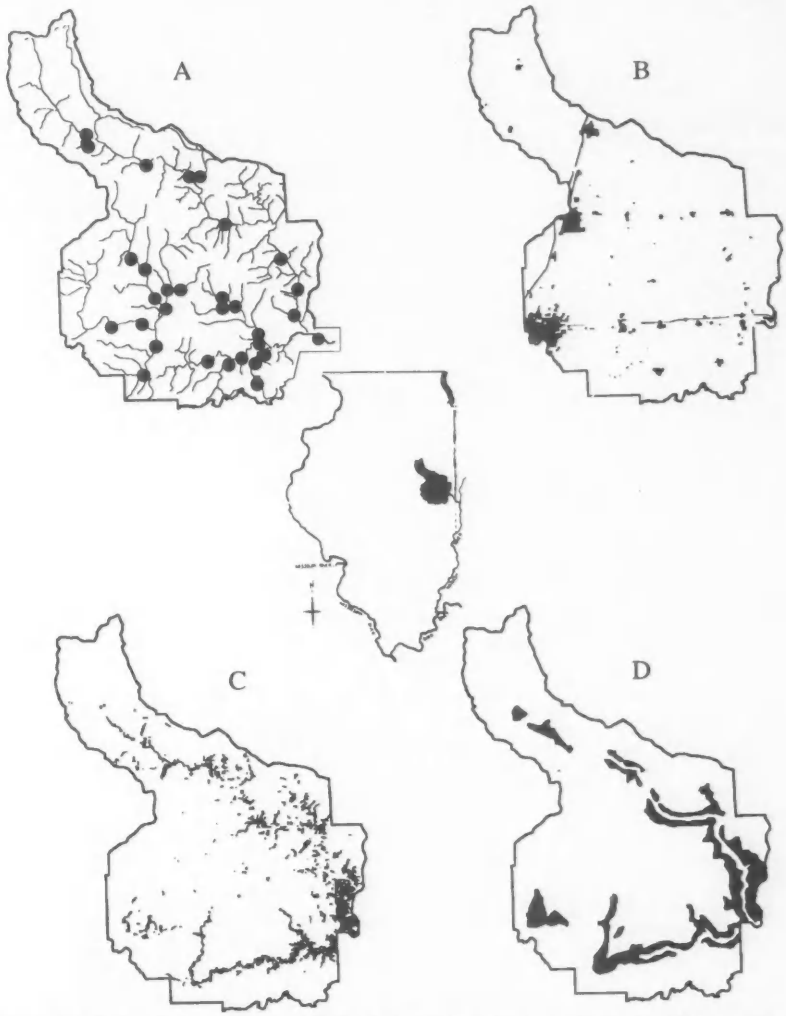

FIG. 1. Salt Fork (south-western) and Middle Fork (north-eastern) watersheds. (A) Major sampling locations. (B) Urban and suburban land-use distributions. (C) Forested land distributions. (D) Forest-derived soil associations, based on interpretations following Follmer (1985). (A–C) are based on photo-interpretation of EROS high altitude photos series 1981 and 1983 (USDA); (D) is based on data from (Fehrenbacker et al. 1984).

ficient (K) were estimated from each data set by least-squares regression of the after-dark data:

$$dC/dt = R + KD,$$

where C is oxygen concentration (mg/L); t is time (h); R is mean respiration rate (mg $O_2 \cdot L^{-1} \cdot h^{-1}$); K is the reaeration coefficient ($1/t$); and D is the oxygen deficit (O_2 at saturation − observed O_2). Gross primary production was then estimated per quarter-hour of daylight from the relation:

$$P_h = (dC/dt) + R - KD,$$

where P_h is gross primary production (mg $O_2 \cdot L^{-1} \cdot h^{-1}$). Daily P was estimated as mean $P_h \times$ hours of daylight. Daily ecosystem respiration (R) was estimated as $24 \times R$. Photosynthestis and respiration rates expressed per unit volume are used in statistical analyses throughout this paper. This is done both to emphasize the fact that measurements are made per unit volume, and to minimize the variance of the metabolism estimates. Conversion to unit area is made by multiplying unit volume estimates by mean channel depth. Since mean channel depth is subject to substantial sampling error and bias, areal estimates are less precise, although often desirable for comparative purposes. Thus we generally report areal estimates, but have used per unit volume rates in most statistical analyses.

Results

Vegetation and Land-Use Structure

The Salt Fork and the Middle Fork watersheds are both heavily agriculturalized, with 91 and 93% of their drainage

TABLE 1. Land-use/cover distributions for the Salt Fork and Middle Fork basins of the Vermilion River.

	Salt Fork basin		Middle Fork basin	
Land use	km²	Percent	km²	Percent
Agriculture	1093	90.8	1033	93.0
Urban	67	5.6	13	1.2
Woodland	34	2.8	60	5.4
Wetland	2	<1	3	0.2
Barren	8	<1	<1	<0.1
Total	1204		1109	

areas, respectively, in intensive rowcrop production (corn and soybeans) (Table 1). However, the two watersheds differ substantially in extent of urbanization (Fig. 1b). Seven urban (primarily residential) areas are located within the Salt Fork watershed, including the cities of Urbana and Rantoul, and the towns of Sidney, St. Joseph, Homer, Muncie, and Oakwood. Only one urbanized area of any size, Paxton, is located within the drainage basin of the Middle Fork. Population centers on the Salt Fork contributed to an overall density of 357 individuals·km^{-2} (138·mile^{-2}) as opposed to a density of 39·km^{-2} (15·mile^{-2}) for the Middle Fork basin. Despite differences in absolute urbanization, the longitudinal distribution of urban land use is similar in both watersheds, with the highest proportional contributions occurring at stations with a drainage of 500–800 km^2 (200–300 miles^2; see Fig. 2).

Significant riparian vegetation was restricted to mature gallery forests on the lower portions of the mainstem in both rivers (Fig. 1c). The original extent of the gallery forests are clearly reflected in the present-day distributions of soil associations within the watersheds (Fig. 1d).

Comparisons of the distributions of forest-derived soils and modern woodlands suggest that, despite a significant narrowing of the gallery forests due to agricultural encroachment, the longitudinal extent of the gallery forests has remained remarkably consistent during the past 140 yr. Deforestation since white settlement had reduced total riparian forest area by approximately 72% in the Middle Fork, and 74% of the Salt Fork watersheds, respectively. However, comparisons of modern forest distributions with presettlement distributions as mapped by both 19th century cartographers and edaphic evidence (Fig. 1d) indicate little change has occurred in the longitudinal extent of the riparian forest. Presently, and we believe historically, both percentages of the watershed forested and of the channel shaded tend to increase in a downstream direction and are significantly correlated with the logarithm of drainage area ($r=0.367$, $P<0.05$ and $r=0.548$, $P<0.01$, respectively). Some small tributary streams (drainage area <25 km^2) are significantly shaded by the channel wall itself, although this is mainly an artifact of early channelization.

Thermal Structure and Turbidity

The Vermilion River drains relatively impermeable soils; as a result, both watersheds receive most of their water from surface and shallow subsurface (field tile) runoff. The small contribution of cold groundwater to total discharge, combined with a lack of shading in upstream reaches, results in a relatively homogeneous average temperature throughout the entire watershed at any given time (correlation with drainage area = 0.059, $P>0.05$). However, observed diel ranges in temperature were highly dependent upon a site's position in the watershed. Daily maximum temperature declined in the downstream direction and was negatively correlated with drainage area ($r=-0.2$, $n=204$, $P<0.01$), but daily minimum temperature increased with drainage area ($r=0.26$, $n=205$, $P<0.01$). Diel temperature fluctuations, therefore, decreased with increasing stream size (i.e. thermal stability increased with increasing flow volume). Temperature variability was highest in the spring and fall with diel ranges sometimes in excess of 15°C. But even during the summer, diel fluctuations of 10°C were frequently observed in the upper parts of the Vermilion watershed.

TABLE 2. Regression analysis of nephelometric turbidity (log transformed NTU) in the Vermilion River watershed for all stations and all dates. Drainage area is in square kilometres; watershed is a dummy variable (0 = Salt Fork, 1 = Middle Fork); flow frequency ranges from 0.0 to 1.0. Model is of the form: $Y=a+b\ln W+c\ln Y+dX$.

Source	DF	SS	MS	F
Regression	3	418.1	139.4	158.2
Residual	427	376.1	0.881	$P<0.0001$
Total	430	794.166		

$r^2=0.53$, standard error = 0.94, coefficient of variation = 41.2

Parameter	Value	T-value	Partial-F
Intercept	2.306	153.44	
ln drainage area	0.088	8.38	70.25
ln flow frequency	−4.314	−19.23	369.74
Watershed (dummy)	0.524	5.71	32.64

Turbidity in the Vermilion River, as in most midwestern rivers, was generally high and variable. Turbidity in weekly sampling ranged from <1 to >600 nephelometric units (NTU). Turbidity increased with increasing discharge ($r=0.53$, $P<0.0001$) and was related statistically both to increased suspended loads associated with high flow events (flows with low exceedence frequency) and to a tendency of increasing turbidity in the downstream direction (Table 2). The Middle Fork watershed was slightly more turbid than the Salt Fork ($T=5.714$, $P<0.001$), particularly during high flows, presumably because of the larger proportion of clayey soils in the upper reaches of its watershed.

Nutrient Availability

Nutrient concentrations were extremely high, but there was a large amount of variability between seasons and between sites (Table 3). Total inorganic nitrogen concentrations ranged from 0.32 to 12.7 mg·L^{-1}, with an annual mean concentration for both watersheds of 4.8 mg·L^{-1}. SRP ranged from 0.003 to 15.2 mg·L^{-1} and averaged 0.6 and 1.5 mg·L^{-1} in the Middle Fork and Salt Fork, respectively. The large-scale distribution of nutrient availability within these watersheds was primarily controlled by land-use patterns, principally urbanization in the case of SRP, and both urbanization and seasonal field applications of fertilizers by farmers in the case of nitrate (Fig. 2). Nitrate concentrations were generally similar in both watersheds with concentrations >5.0 ppm not uncommon. During summer and fall, the highest concentrations of nitrate were associated with urban areas (appearing as vertical streaks in Figs. 2c and especially 2f), representing point-source inputs. Concentrations in the Salt Fork were generally higher than those in the Middle Fork during these periods, due to greater urbanization.

TABLE 3. Some representative mean summer (July–September, 1984 and 1985) values for key nutrient, chemical, and biological parameters in the Vermilion River watershed. P = gross primary productivity; R = ecosystem respiration. — denotes insufficient data for a seasonal mean. Drainage area given in square kilometres.

	Drainage		Diel variation					P	R
Station	Area	Order	NO_3 mg/L	SRP mg/L	Turbidity (NTU)	Temperature range°C	O_2 range ppm	g O_2/m^2d	
11	199	4	6.03	4.92	10.29	4.1	2.72	11.0	24.1
12	217	4	6.4	4.67	4.56	5	5.05	8.6	8.5
13	126	4	4.18	1.92	4.13	9.6	12.4	35.8	24.9
15	26	3	2.42	0.18	3.96	8.7	6.2	6.4	11.51
18	59	3	2.7	0.25	5.88	9.9	4.3	11.4	11.5
19	10	1	2.78	0.16	14.36	9.3	4.2	10.2	9.7
21	235	4	4.08	1.45	2.53	8.2	16.3	44.2	18.9
24	378	5	4.11	1.04	10.57	6.7	—	14.6	41.6
29	21	1	4.1	0.16	22.02	—	—	<.1	34
30	84	3	4.21	0.11	18.87	—	—	<.1	13
33	176	4	3.49	0.25	14.12	4.1	—	9.4	17
34	1023	5	4.23	2.34	30.79	2.7	4.42	2.9	12.7
49	7	1	6.57	0.17	7.96	8.7	2.27	5.1	6.2
50	221	4	4.86	0.21	13.16	6.8	3.4	13.4	21.8
53	473	5	4.62	0.99	18.76	3.9	5.59	15.85	14.05
54	555	5	4.19	0.45	41.72	—	2.09	6.15	10.6
55	42	4	2.77	0.2	7.22	5.1	—	8.533	18.77
57	739	5	3.38	0.52	50.16	—	5.66	17	18.45
59	1021	6	3.43	0.44	100.8	6.1	—	1.467	23.333
84	619	5	4.99	3.36	9.49	5.2	4.51	10.65	13.5
89	890	5	4.73	2.5	19.07	2.6	0.7	5.47	14.47
95	61	2	3.93	0.14	6.05	4.1	2.41	5.7	13.83
96	55	2	4.29	0.15	2.43	6.1	5.48	15.5	15.43
98	1130	6	2.89	0.35	—	3.1	3.65	6.975	10.67
99	3505	7	3.82	1.23	—	8.2	2.1	4.267	8.26

However, from late fall through the high-water period in late spring-early summer, nitrate was extremely high throughout both watersheds. The second period coincided with agricultural ammonia applications, which begin in November–December, peak in May, and are completed in June.

SRP concentrations were highly correlated with urbanization. During low-flow periods in the Salt Fork, concentrations downstream of urban effluent inputs routinely exceeded 5 ppm; these reaches appear as vertical streaks in the SRP watershed profiles (Figs. 2b and 2e). During low-flow periods, high concentrations in the SRP profile tended to "bleed" downstream. During high flow, this longitudinal patterning is diluted. The Middle Fork basin had little urbanization and relatively low SRP concentrations. Although SRP exceeded 5 ppm at times in the vicinity of the only population center, concentrations generally ranged from 0.2 to 1 ppm, low by Vermilion River standards but still high in comparison with most forested and desert streams in North America (Omernick 1977).

Ecosystem Metabolism

Rates of gross primary productivity varied from below detection limits to >50 g $O_2 \cdot m^{-2} \cdot d^{-1}$ (>15 g carbon$\cdot m^{-2} \cdot d^{-1}$). Rates were highest during summer and in the upper portions of the watershed (Fig. 3). The seasonal pattern in gross photosynthetic production was similar in both sub-watersheds. In spring, P rose first in the upstream reaches with drainage areas of 20–100 miles^2. By June, P exceeded 10 g $O_2 \cdot m^{-2} \cdot d^{-1}$ in almost all first- and second-order streams, and by August high levels of photosynthesis could be found throughout the watershed. As water temperatures declined in the fall, rates of P declined, first in the upstream reaches and finally to <2 g $O_2 \cdot m^{-2} \cdot d^{-1}$ throughout the entire watershed by December.

Multiple regression analyses indicated that water temperature and light availability (as mediated by turbidity and shading) were the primary variables controlling rates of primary production (Table 4). A combination of temperature, turbidity, depth (depth × turbidity is proportional to extinction coefficient), and maximum percentages of the channel shaded explained 61% of the variance in 195 observations across all months, over 30 sites, and two watersheds. When data from only the summer growing season were used in the analysis, temperature was not significant, and turbidity and shading explained most of the variation in P ($r^2 = 0.77$, $P < 0.0001$) (Table 5). Neither N nor SRP (nor their transformations) could be correlated with the residuals of these fits, suggesting that nutrient limitation in this watershed is unimportant. In exploratory single-station analyses, nitrate concentrations were found to be negatively correlated over time with P at a few highly photosynthetic sites. This likely reflects high rates of nutrient removal but does not necessarily indicate N limitation. No significant difference between the Salt Fork and Middle Fork basins was found, unless turbidity, which was higher in the Middle Fork, was removed from the regression. In both analyses, the relationship of each key variable to P was best described as a power function of the form:

(1) P per unit area = $aT^{+b}\text{NTU}^{-c}S^{-d}Z^{+e}$,

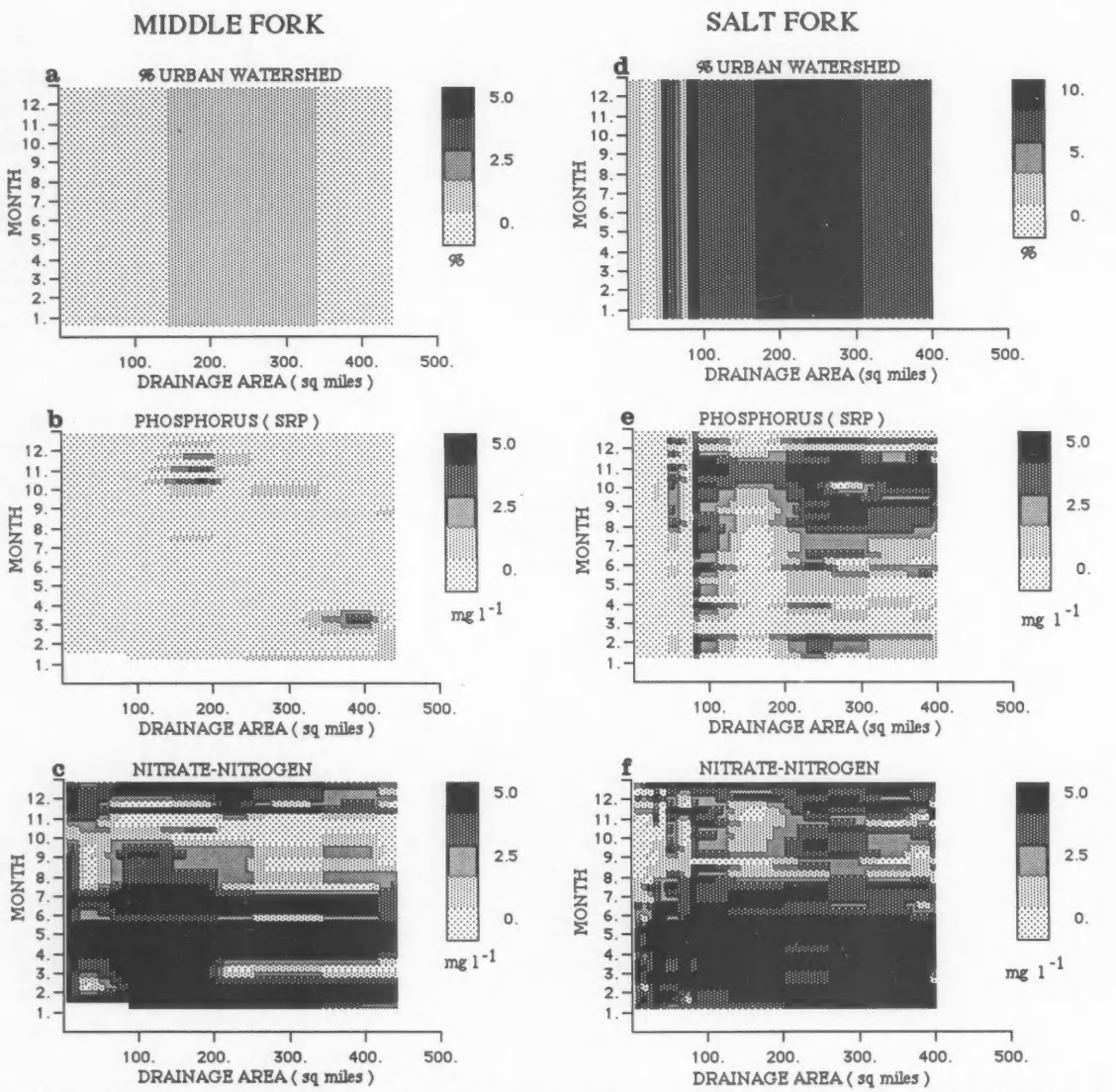

FIG. 2. Watershed profiles for urbanization, SRP and nitrate-N concentrations. Grayscale interpolation is based on 1024 samples collected between January 1984 and December 1985. Vertical axes represents time (month) and horizontal axes represent position in the drainage basin; upstream is to the left and downstream to the right.

where P is gross primary productivity (g $O_2 \cdot m^{-2} \cdot d^{-1}$); T is temperature (°C); NTU is turbidity (nephelometric units); S is maximum percentage of channel shaded; and Z is mean (hydraulic) depth (m); and a,b,c,d, and e are coefficients of the indicated sign.

Respiration rates ranged from undetectable to 177 g $O_2 \cdot m^{-2} \cdot d^{-1}$ and were highly correlated with photosynthetic rates ($r = 0.534$, $N = 218$, $P < 0.001$, log transformed). Multiple regression analyses of respiration data were less successful than those for photosynthetic rate data. Although r^2-values were generally lower than those in the P regression, statistically significant models of biologically reasonable form (Tables 6 and 7) were generated:

$$(2) \quad \text{R per unit area} = aP^{+b}T^{+c}Z,$$

where R is ecosystem respiration (g $O_2 \cdot m^{-2} \cdot d^{-1}$). As in the case of photosynthesis, when the analysis was based on mean summer rates, the temperature effect was no longer significant but the fit was substantially improved ($r^2 = 0.69$, $P < 0.0001$; Table 7).

The ratio of P to R, an index of relative autotrophy, was highly variable between seasons and between sites. During the summer (July–September), 60% of the sites examined had a P:R ratio <1, while 40% could be classified as autotrophic. This percentage closely approximates the relative frequency of autotrophy in all summer observations and is higher than the frequency of autotrophy when observations from all seasons

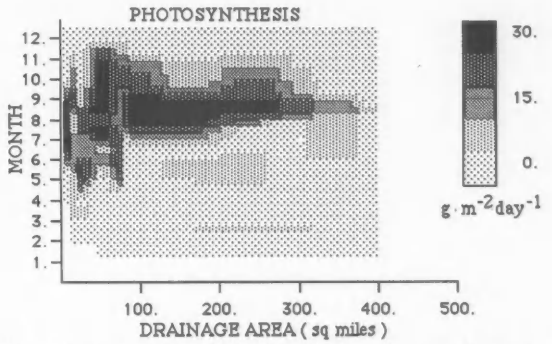

FIG. 3. Seasonal and longitudinal distribution of gross primary production rates (g $O_2 \cdot m^{-2} \cdot d^{-1}$) for the Salt Fork watershed. Grayscale interpolation is based on 205 samples collected between January 1984 and October 1986. Vertical axes represents time (month) and horizontal axes represent position in the drainage basin; upstream is to the left and downstream to the right.

TABLE 4. Regression analysis of gross daily primary production, P (g $O_2 \cdot m^{-3} \cdot d^{-1}$) in the Vermilion River watershed for all stations and all dates. Model is of the form: $\ln(P+1) = a + b$ lnNTU $+ c\ln Z + d\ln T + e\ln S$. Where NTU is nephelometric turbidity; Z is mean depth; T is daily mean temperature; S is daily maximum percent channel shaded. To express P per unit area (g $O_2 \cdot m^{-2} \cdot d^{-1}$, the regression coefficient for depth becomes $+0.317$ (i.e. $-0.683 + 1$).

Source	DF	SS	MS	F
Regression	4	229.4	57.4	73.8
Residual	191	148.4	0.778	$P<0.0001$
Total	195	377.9		

$r^2 = 0.61$, standard error = 0.88, coefficient of variation = 46.3

Parameter	Value	T-value	Partial-F
Intercept	0.804	2.97	
ln turbidity	−0.421	−6.53	42.59
ln depth	−0.683	−5.98	35.79
ln temperature	0.727	9.532	90.85
ln percent shaded (+1)	−0.534	−1.578	2.49

TABLE 5. Regression analysis of gross daily primary production, P (g $O_2 \cdot m^{-3} \cdot d^{-1}$) in the Vermilion River watershed. Mean rate from major stations for summer (July–September) only. Model is of the form: $\ln(P+1) = a + b\ln\text{NTU} + c\ln Z + d\ln S$. Where NTU is nephelometric turbidity; Z is mean depth; S is daily maximum per cent channel shaded. To express P per unit area (g $O_2 \cdot m^{-2} \cdot d^{-1}$) the regression coefficient for depth becomes $+0.555$ (i.e. $-0.455 + 1$).

Source	DF	SS	MS	F
Regression	3	17.2	5.73	18.7
Residual	17	5.21	0.307	$P<0.0001$
Total	20	22.41		

$r^2 = 0.77$, standard error = 0.55, coefficient of variation = 19.3

Parameter	Value	T-value	Partial-F
Intercept	4.008	8.233	
ln turbidity	−0.369	−2.70	7.31
ln depth	−0.455	−1.84	3.37
ln percent shaded (+1)	−2.541	1.837	13.28

TABLE 6. Regression analysis of ecosystem respiration rate, R (g $O_2 \cdot m^{-3} \cdot d^{-1}$) in the Vermilion River watershed. Model is of the form: $\ln R = a + b\ln(P+1) + c$ lnT. For R per unit area (g $O_2 \cdot m^{-2} \cdot d^{-1}$) $R = a(P+1)^b X^c Z$, where Z is mean depth.

Source	DF	SS	MS	F
Regression	2	70.99	35.5	46.33
Residual	215	164.71	0.77	$P<0.0001$
Total	217	235.70		

$r^2 = 0.27$, standard error = 0.903

Parameter	Value	T-value	Partial-F
Intercept	1.601	8.03	
ln photosynthesis	0.344	6.674	44.54
ln temperature	0.185	2.135	4.56

TABLE 7. Regression analysis of ecosystem respiration rate, R (g $O_2 \cdot m^{-3} \cdot d^{-1}$) in the Vermilion River watershed. Mean values for major stations for summer (July–September) only. Model is of the form: $\ln R = a + b\ln(P+1)$. For R per unit area (g $O_2 \cdot m^{-2} \cdot d^{-1}$) $R = a(P+1)^b Z$, where Z is mean depth.

Source	DF	SS	MS	F
Regression	2	5.93	5.93	39.43
Residual	21	3.16	0.14	$P<0.0001$
Total	22	9.09		

$r^2 = 0.65$, standard error = 0.39

Parameter	Value	T-value	Partial-F
Intercept	1.903	8.377	
ln photosynthesis	0.493	6.28	39.43

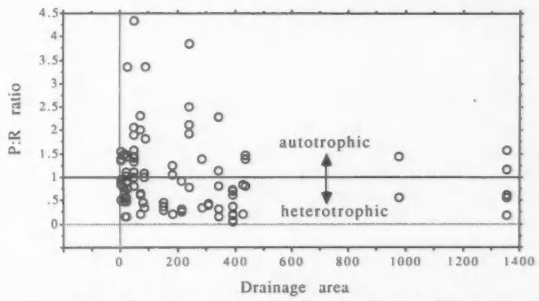

FIG. 4. Longitudinal distribution of P:R ratios (total daily gross primary production to total daily ecosystem respiration) during summer (July–September) months of 1985 and 1986.

were pooled (31%). There was a clear longitudinal pattern in the P:R ratios, with most autotrophic sites occurring high in the watershed (Fig. 4). This observation is consistent with the expected distribution arising from equations (1) and (2), because the ratio of depth dependencies for P and R per unit area is a power function with a negative exponent. However, the variances in these data were high, and low ratios were not uncommon in the upper watershed. This variation indicates that other controlling variables (temperature, shading, and turbidity) can and do vary independently of depth.

Discussion

Nutrient levels in the Vermilion River were surprisingly high, even for an agricultural stream in this region. Omernik's (1977)

TABLE 8. Representative values for daily gross photosynthetic rate (P) (g $O_2 \cdot m^{-2} \cdot d^{-1}$).

P	Biome type	Climate	Source
5–18	Deciduous forest	Mesic	Edwards and Owens (1962)
<1–9	Deciduous forest	Mesic	Hall (1972)
1–12	Deciduous forest	Mesic	Bott et al. (1985)
<1–1	Coniferous forest	Mesic	Naiman and Sedell (1981)
<1–3	Coniferous forest	Mesic	Duncan and Brusven (1985)
4–48	Grassland	Mesoxeric	Duffer and Dorris (1966)
1–32	Grassland	Mesoxeric	Prophet and Ransom (1974)
<1–65	Grassland	Mesoxeric	present study
8–12	Desert	Xeric	Minshall et al. (1985)
<1–22[a]	Desert	Xeric	Busch and Fisher (1981)
14–27	Desert	Xeric	Cushing and Wolf (1984)

[a]Based on reported hourly values × 10h of effective daylight.

survey of land-use relationships to instream water quality suggests that mean annual concentrations of total inorganic nitrogen usually range from 2.87 to 6.64 $mg \cdot L^{-1}$ for midwestern streams with 100% of their watersheds in agricultural and urban land use. The annual mean concentration in the Vermilion River of 4.8 $mg \cdot L^{-1}$ is within this range. Phosphorus concentrations, on the other hand, are substantially higher than Omernik's (1977) predicted range of 0.073–0.251 $mg \cdot L^{-1}$ for total P. SRP concentrations alone averaged 0.6 and 1.5 $mg \cdot L^{-1}$ in the two river basins examined, with maximum concentrations exceeding 5 $mg \cdot L^{-1}$. Agricultural activity is usually cited as the primary cause of high nutrient conditions in streams of the "corn belt" (Kilkus et al. 1975; Omernik 1977; Goldman and Horne 1983). Soil erosion, in particular, commonly has been identified as the major contributor of phosphorus to agricultural watersheds. Although soil-borne phosphorus (usually organic) contributes large portions of the annual transported load in many streams, most of this transport takes place over very short intervals following major hydrologic events (Baker 1984). Data from the Vermilion River suggest, however, that for average instream conditions urban, rather than agricultural land-use patterns control the longitudinal distribution of SRP concentrations. Urban areas (point and nonpoint sources are indistinguishable) clearly dominate the watershed profiles for SRP and for nitrate during most of the growing season, elevating concentrations two to five times the background levels (Fig. 2). Agricultural inputs of nitrogen were detectable and clearly controlled instream concentrations during late fall–early spring, corresponding to periods of very low temperature and/or high water levels and minimal biological activity.

Factors Limiting Primary Production

Although gross photosynthetic rates in the Vermilion River were variable, observed maximums were as high or higher than previously reported values for agriculturalized grassland biomes (Table 8). Streams draining temperate grasslands tend to be more productive than streams that drain forested or more arid watersheds. This productivity can be attributed to a combination of factors, the most important of which is that their shallow, warm headwaters are open to light. Furthermore, as is clearly the case in the Vermilion River, these streams are rich in phosphorus and nitrogen.

While photosynthetic rates were highest in the smaller headwater streams, not all low-order streams were highly productive. This variability in photosynthetic production between sites of a similar drainage area was largely due to differences in shading. There was a striking difference between photosynthetic rates of reaches high in the drainage network and of mainstem tributaries of the same order which entered the main river valley passing through its associated gallery forests. For example, station 95 (second order) was located on a small tributary to the main stem of the Vermilion River and had a drainage of 54 km^2. Because the stream flows into the Salt Fork at a point where it is a fifth-order river, much of its lower reach is enveloped in extensive gallery forest, and this site was consequently heavily shaded. The mean summer photosynthetic rate at station 95 was 5.7 g $O_2 \cdot m^{-2} \cdot d^{-1}$. Station 18 had a similar-sized watershed (62 km^2, second order), but it was located in the upper portion of the Salt Fork drainage network, quite removed from the influences of the gallery forests. At this site the mean summer rate of photosynthesis was 11.4 g $O_2 \cdot m^{-2} \cdot d^{-1}$, twice as high. Thus, it is not possible to accurately characterize the relationship between stream size (drainage area or stream order) and expected rates of primary production without also specifying assumptions about inputs of radiant energy.

In the Vermilion River drainage, nutrient availability appeared to have little importance in controlling the longitudinal distribution of photosynthetic rates. No significant positive correlations were found between P and nitrate-N or SRP concentrations, either on an annual basis or when data from only summer (June–September) were examined. Recent nutrient addition experiments (Munn et al. 1989) at seven sites in these watersheds also support the hypothesis of no nutrient limitation. Light availability, as mediated by turbidity, depth, and shading, appears to be the primary limiting factor that controls the large-scale pattern of photosynthesis in the Vermilion River.

Several factors interact and together control the amount of radiant energy available for instream photosynthesis. Shading by riparian vegetation has been most often identified as the key light-limiting factor in stream ecosystems (Vannote et al. 1980; Cummins et al. 1984). However, in the Vermilion River, as presumably in most turbid rivers, light extinction due to scattering is equally important. The amount of light extinction that occurs is a function of both the light scattering capacity of water (turbidity) and the distance light must travel in water (depth). In limnological investigations, light extinction has historically been measured empirically and described in terms of an exponential decay ($dL/d\ depth = -k \cdot L$; where L is light intensity or irradiance). The decay coefficient, k, is then used as an index of light extinction (Hutchinson 1957). Nephelometric turbidity is a routinely measured parameter in water quality surveys that

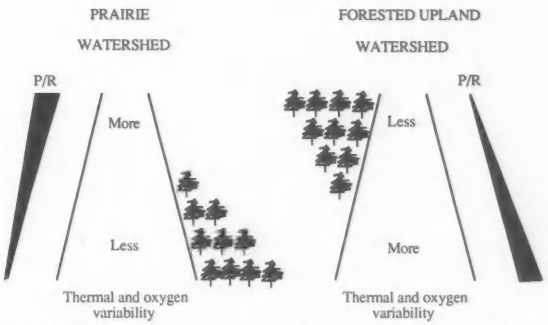

FIG. 5. Summary of organizational differences between grassland and forested watersheds.

can be used as a functional analog of the extinction coefficient. Light availability in our empirical model for P is represented by the composite $NTU^{-c}S^{-d}Z^{+e}$. This term encompasses three independent parameters that control the amount of light which can penetrate to periphyton communities on the channel bottom: shading, depth, and turbidity. Examination of the partial sums of squares from the regressions (Tables 4 and 5) gives some indication of the relative importance of these three terms in the Vermilion River. In the analysis of the entire data set (Table 4), the shading variable adds very little to the overall regression, suggesting that, on an annual basis, a very large portion of the variance in photosynthesis is related to seasonal cycles in temperature and high water. If mean summer P values for each station are used, and the analysis restricted to the summer growing season when shading effects are at a maximum and turbidity at a minimum (Table 5), the shading variable and turbidity effects (depth and NTU) are roughly equivalent (partial F's = 13.3, 7.3, and 3.4 for shading, turbidity, and depth, respectively). Thus, we conclude that overall turbidity is at least as important as riparian shading in limiting light availability to this particular system.

Prairie Watersheds and the RCC

Clearly the large-scale structure of the Vermilion River watershed is quite different from the typical structure of watersheds in temperate forested uplands. Longitudinal distributions of riparian vegetation, temperature, and ecosystem metabolism (P and R) are basically inverted (Fig. 5).

The upper portions of the watershed, which drain former wet prairie lands, are open and unforested and have been so prior to white american settlement in the 1840's. Gallery forests and attendant leaf inputs eventually develop along the drainage network but are restricted to the lower half of the watershed. This situation is exactly the reverse of the "prototype" configuration posited by Cummins et al. (1984) for nonxeric river systems. Open headwaters are more typical of xeric regions like deserts, high altitudes, etc. (Cummins et al. 1984; Busch and Fisher 1981). Prairies and other grassland ecotypes are mesoxeric systems and owe their peculiar vegetational structure to this fact as well as to high rates of disturbance.

High ratios of groundwater to run-off are common in upland systems and usually result in marked downstream temperature gradients (Vannote et al. 1980; Minshall et al. 1985), with diel variability increasing in the downstream direction. In the Vermilion River, groundwater input is relatively low and there was very little longitudinal variation in median temperature. Diel variability, in the absence of the moderating influence of groundwater, was highest high in the watershed and declined with increasing drainage area. Without a riparian canopy, the low flow volumes (with reduced thermal capacitance) at upstream sites tended to move quickly towards a thermal equilibrium with air temperature, mimicking diel fluctuations in the terrestrial environment. Downstream, larger thermal capacitance is augmented by insulating tendencies of the riparian canopy; together, they damp the thermal response of the river to diel changes in radiation inputs. Thus, differences between the thermal characteristics of this river and those of typical boreal rivers result both from regional characteristics of the hydrology and from the unique structuring of riparian vegetation in prairie watersheds.

Given the higher daytime temperatures and absence of shading vegetation, it is not surprising that we found the highest rates of autotrophic production in the upper reaches of this watershed. Forested upland watersheds are usually described as being heavily heterotrophic in their upper reaches, with autotrophic activity increasing in mid-order streams where the river is wide enough to break the canopy cover and admit more light to the water's surface (Cummins 1974; Minshall 1978; Vannote et al. 1980; Minshall et al. 1985). Photosynthetic activity declines further downstream as increasing depth and turbidity reduces light. In the Vermilion River, the most photosynthetically active sites occurred at sites with drainage areas of <260 km^2 (first-third order). Beyond that point, a combination of depth, turbidity, and forest canopy reduce light inputs significantly and resulted in a corresponding decline in P per unit stream area. Although channel shading began to wain beyond 770 km^2, no significant increase in photosynthetic activity was detected, presumably because of light extinction due to turbidity and increased depth.

In its simplest form, the RCC posits a pristine structure for river ecosystems that begins with heterotrophic headwaters dominated by allochthonous inputs from riparian vegetation, grades into an autotrophic middle section, and ends in a large river that is again primarily heterotrophic (Vannote et al. 1980). In the Vermilion River, as we have demonstrated, the longitudinal pattern of ecosystem metabolism is distinctly different. However, recent elaborations of the RCC (Cummins et al. 1984; Minshall et al. 1985) have more flexibly addressed the relationship between stream metabolism and patterns in riparian vegetation. While a continuum of dominant energy sources is still proposed (allochthonous production to autochthonous production to lateral and upstream accrual), individual streams are considered to enter this continuum at different points; xeric systems are described as entering the continuum below the zone of shading and allochthonous input from riparian forests (Minshall et al. 1985). Desert rivers, then, are viewed as having high P:R ratios in their upstream reaches, with instream periphyton production being replaced first by macrophyte production and finally by floodplain and upstream accrual. This expanded version of the RCC, by stressing the controlling role of riparian vegetation, could be said to predict the upstream autotrophy prevalent in xeric systems and in mesoxeric systems like the Vermilion River.

On the other hand, the downstream sequencing of carbon sources in the Vermilion River still is not consistent with the predicted sequence. While upstream autotrophy was common (but not universal), the development of extensive gallery forests downstream means that terrestrial leaf carbon inputs are not absent but simply displaced longitudinally; that is, the allo-

chthonous to autochthonous sequence from deciduous forests has been inverted but not shortened as the RCC predicts. Downstream declines in photosynthetic rate per unit area coincide with increased inputs of terrestrial litter, and this increase is mirrored in the increasing number of shredders occurring in downstream communities (M. J. Wiley and L. L. Osborne, unpubl. data). Furthermore, the emphasis of the RCC on the riparian controls of photosynthesis fail to give proper emphasis to the importance of turbidity. As previously discussed, on a strictly statistical basis it can be argued that turbidity was more important than channel shading in explaining the longitudinal distribution of photosynthetic rates.

The tremendous influence of the RCC on North American stream ecology arises from its pioneering perspective, which formally links the biological structure and geomorphological structure of whole river systems. However, the RCC has difficulty describing rivers like the Vermilion because it relies largely upon description rather than mechanism to understand river ecosystem structure. There is simply no single generalization about ecosystem structure that can unambiguously describe the large variety of river systems known to exist. Our goal in theory development should not be to reduce data to a single, all-sufficient, qualitative generalization, but instead it should be to develop a set of quantitative relationships (i.e. a model) that, when given an array of inputs, can accurately predict the diversity of structures we observe in nature.

In this regard, simple empirical relationships between major driving variables and system variables of interest, may be a far more practical basis for predictive modelling of lotic ecosystem structure. A useful example of the potential power of this approach is the hydraulic geometry commonly used by geomorphologists, hydrologists, and engineers. Stream width, hydraulic depth, mean velocity, and channel cross-sectional area (W, Z, V, and C, respectively) can all be expressed as power functions of discharge at a single site (Leopold and Maddock 1953; Stall and Fok 1968; Stall and Yang 1968) or for entire watersheds as functions of drainage area and flow exceedence frequency (the frequency or probability that a flow of a given magnitude will be exceeded based on hydrographic records). For example, basin hydraulic geometry predits that mean hydraulic depth for any site in a watershed is given by:

$$(3) \quad Z = e^{aF}A^{b}$$

where F is flow frequency, A is drainage area, and a and b are basin-specific coefficients. Similar functions describe related hydraulic variables:

$$W = \text{Width} = e^{cF}A^{d}$$
$$V = \text{Velocity} = e^{gF}A^{h}$$
$$C = \text{Cross sectional area} = e^{vF}A^{z}.$$

These systems of descriptive equations reflect known relationships between driving variables (e.g. the hydraulic continuity equation: $Q = W \cdot V \cdot Z$) and can be empirically parameterized for specific watersheds or sites. This approach has provided a set of powerful tools for predicting and describing the hydraulic characteristics of both cross-sections and drainage networks, tools which are frequently used in geomorphological and hydrological research and in fluvial engineering (Thomann 1972).

Simple, empirically constructed models of key biological variables such as equations (1) and (2), when combined with the physical descriptors from hydraulic geometry, may provide a useful prototype of a quantitative theory for stream ecology.

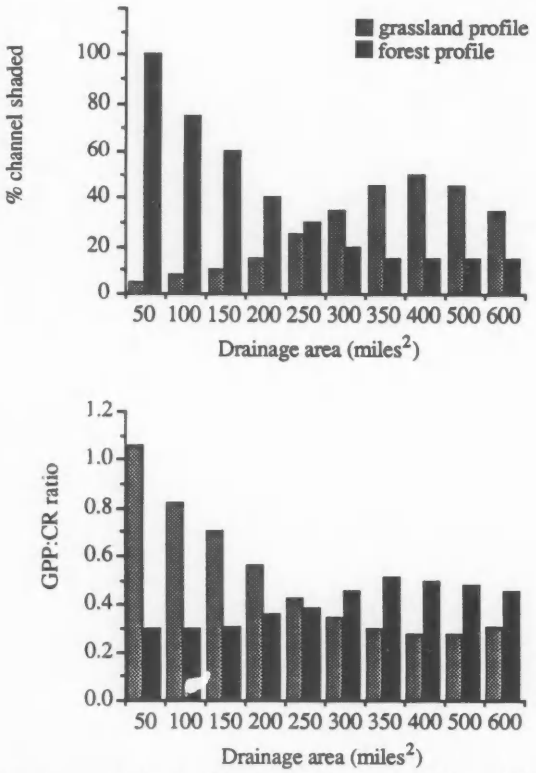

FIG. 6. An example of predicting longitudinal structure from profiles of riparian vegetation. Upper panel; typical shading profiles for forested and grassland watersheds. Lower panel; predicted ratios of total daily gross primary production to total daily ecosystem respiration based upon equations (1), (2), and (3) (in text) and shade profiles above. Turbidity and temperature were assumed constant for the purpose of illustration, depth was estimated using published hydraulic geometry relations for the Vermilion River (Stall and Fok 1968).

For example, we have used equations (1), (2), and (3) above, parameterized by least squares (see Tables 5 and 7) to make predictions about the longitudinal profile of ecosystem metabolism characteristic of either a deciduous forest or a grassland biome watershed (Fig. 6). In this analysis, we used arbitrary but typical shading profiles for each biome type (Fig. 6 top) as input to equations (1) and (2), along with depth calculated from the hydraulic geometry (equation (3)). Temperature and turbidity were held constant to simplify the example.

In the deciduous forest profile, we assumed shading was highest in the uppermost portions of the watershed, with the canopy becoming more and more open downstream (Fig. 6, top, solid bars). Resulting P/R ratios are distributed much as the classic RCC described them. Ratios are low in the upper watershed, increase to a maximum in middle-order reaches, and decline slowly as the river becomes larger (Fig. 6, bottom, solid bars). In the prairie profile, we assumed little shading in the headwaters, but, with the development of the gallery forests, light penetration declines in the middle reaches (Fig. 6, top, hatched bars). The metabolic profile derived from ths assumption differs substantially from that of the forest (Fig. 6, bottom, hatched bars). P/R ratios are highest in the headwaters and

decline sharply with increasing depth and shading. Loss of shading downstream is offset by increased depth, and only a slight increase in autotrophy is predicted.

The differences predicted between forested and prairie profiles arise from the different longitudinal profiles of a key driving variable (in this case, shading or light availability), and are generated by a single set of predictive equations. Note that in this type of model the driving variables need not be distributed in any particular manner. Therefore, this approach does not necessarily posit a "continuum" in either driving variables or lotic system response. Nevertheless, it is consistent with the RCC in that, given a continuous gradient of driving variables (e.g. depth or forest cover), P and R will have predictable longitudinal profiles without strong discontinuities.

We are not suggesting here that any particular equation or model should be universally adopted. Equation (1), for example, has no terms for nutrient limitation since in the Vermilion photosynthesis is not nutrient limited. But, nutrient supply is a limiting factor in many other river systems; clearly a nutrient term would be needed in any more broadly applicable equation. Nor is the form of the expression particularly important. Exponential functions have found wide application in the hydraulic geometry, and provided adequate fits to our data here, but any empirically justifiable function could be used in a similar fashion.

The important point here is that models which incorporate key, driving variables can provide a basis for predicting and explaining the diversity of structures we can observe, whereas generalized descriptions cannot. Modelling the way in which driving variables (depth, temperature, light availability, etc.) are related to whole system function (photosynthesis, respiration) appears to yield greater insight into the structure of stream ecosystems than does generalization about the whole system itself (as in the RCC's search for a valid generalization or "prototype"). In this case, a moderate dose of reductionism can lead to improved predictability in stream ecosystem theory. Furthermore, for grasslands, savannahs, and possibly xeric sites in general, only analysis at a lower level of organization allows us to see the underlying similarities between these kinds of watersheds and the more familiar mesic watersheds of forested and alpine biomes. This is because the similarities are mechanistic, not structural. Prairie rivers and their agricultural descendants are structurally different from forested rivers, just as desert watersheds are structurally different from alpine watersheds. It is not in spite of, but because of these differences, that the careful comparative study of fluvial systems will prove valuable in the elucidation of theory for lotic ecology.

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Causes of Density-Dependent Catchability for Georges Bank Haddock *Melanogrammus aeglefinus*

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Crecco, V., and W. J. Overholtz, 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. 47: 385–394.

We used population estimates (VPA) fishing effort and catch data for Georges Bank haddock, *Melanogrammus aeglefinus*, from 1964 through 1984 to test Paloheimo and Dickie's hypothesis which predicts: (1) that the catchability coefficient (q) from the commercial fishery is inversely related to haddock stock size (N) and stock area (Area); (2) that commercial catch per effort (C/f) data are curvilinearly related to stock abundance; and (3) that search time in the Georges Bank haddock fishery is inversely related to stock abundance. The catchability coefficients for the Georges Bank trawl fishery were inversely related to haddock stock size ($r = -0.82$, $P<0.001$) and stock area ($r = -0.75$, $P<0.001$). There was also a significant curvilinear relationship between commercial C/f and absolute and relative haddock stock biomass from 1964 through 1984. The slope estimate ($B+1$) from this relationship was less than 1.0 ($t = 4.18$ to 8.95, $P<0.001$), indicating nonlinearity between C/f and N. Finally, the relative search time expended by the haddock commercial fishery was inversely related to stock size from 1964 through 1984 ($r = -0.75$, $P<0.001$). These results are consistent with the three predictions of the Paloheimo and Dickie hypothesis, suggesting that fishing mortality rates on Georges Bank haddock are a depensatory function of stock biomass.

Des données sur des estimations de population, sur l'effort de pêche et sur les prises relatives à l'aiglefin (*Melanogrammus aeglefinus*) et recueillies de 1964 à 1984 ont permis de vérifier l'hypothèse de Paloheimo et Dickie selon laquelle (1) la capturabilité (q) dans la pêche commerciale est en corrélation négative avec les effectifs (N) d'aiglefin et la superficie du stock, (2) les données sur les prises commerciales par unité d'effort (C/f) sont en corrélation curvilinéaire avec l'abondance du stock et (3) le temps de prélèvement sur le banc Georges est en corrélation négative avec l'abondance du stock. La capturabilité dans le cas de la pêche au chalut sur le banc Georges était en corrélation négative avec les effectifs d'aiglefin ($r = -0{,}82$, $P<0{,}001$) et la superficie du stock ($r = -0{,}75$, $P<0{,}001$). On notait aussi une relation curvilinéaire importante entre les prises commerciales par unité d'effort (C/f) et la biomasse absolue et relative des effectifs d'aiglefin disponibles de 1964 à 1984. La pente déterminée ($B+1$) à partir de cette relation était inférieure à 1,0 ($t = 4{,}18$ à $8{,}95$, $P<0{,}001$); ceci révèle une corrélation non linéaire entre C/f et N. Le temps de prélèvement relatif consacré à la pêche commerciale de l'aiglefin était en corrélation négative aux effectifs présents de 1964 à 1984 ($r = -0{,}75$, $P<0{,}001$). Ces résultats s'accordent avec les trois prévisions de l'hypothèse de Paloheimo et Dickie, ce qui porte à croire que les taux de mortalité par pêche de l'aiglefin du banc Georges est une fonction anticompensatoire des effectifs du stock.

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It is widely recognized in marine fisheries management that control of fishing mortality rates (F) is essential to prevent recruitment overfishing (Pope 1980; Rothschild 1986). Many fisheries management commissions (eg. NAFO and ICES) attempt to restrain fishing rates at or below some desired reference level (eg. F_{max}, $F_{0.10}$, F_{MSY}) by limiting the efficiency of commercial fishing operations or including gear restrictions and area closures (Clark and Mangel 1979; Saville and Bailey 1980). The effectiveness of effort control depends mainly on the assumption of proportionality between fishing mortality rates (F) and fishing effort (f):

(1) $F = qf$,

where the catchability coefficient (q), the fraction of the fish stock removed per unit of fishing effort, is constant (Gulland 1964; Garrod 1964). If this assumption is satisfied, fishing mortality rates (F) can be manipulated directly through fishing effort regulations, and stock abundance (N) can be monitored annually by changes in commercial catch per unit of effort (C/f):

(2) $C/f = qN$.

The assumption of constant q, however, is seldom satisfied due to seasonal changes in stock availability to the fishery, gear selectivity, gear saturation, and other factors (Pope and Garrod 1975). Moreover, Paloheimo and Dickie (1964) were the first

to show that for the most fish stocks, q varies inversely with both stock abundance (N) and geographical area occupied by the stock. They, and more recently Winters and Wheeler (1985), found that the geographical range inhabited by exploited stocks gets smaller as stock abundance declines. Since fleet communications and electronic detection devices allow most pelagic and groundfish fisheries to easily locate and exploit discrete schools of fish, Paloheimo and Dickie argued that q rises as stock size declines because each unit of fishing effort removes a higher fraction of the available stock when the stock is less abundant and confined to a smaller geographical area. This results in C/f being curvilinearly related to stock abundance (N).

Paloheimo and Dickie (1964) also hypothesized that search time of most modern fisheries rises as stock size declines. If, when fish abundance is high, fishermen spend a greater percentage of a fishing effort (trip) handling their catch, there will be less time spent searching. Paloheimo and Dickie (1964) and Condrey (1984) both attributed the curvilinear relationship between C/f and N to the inverse relationship between search time and stock abundance.

If the Paloheimo and Dickie hypothesis applies to most modern marine fisheries, commercial catch and effort data would seriously overestimate relative stock size and underestimate fishing mortality rates at low stock levels, when the need for unbiased abundance and fishing mortality rates are most vital to stock assessments. Given the widespread reliance on commercial catch and effort data in stock assessments, a rigorous examination of the Paloheimo and Dickie (1964) hypothesis is warranted for most exploited fish stocks. Although an inverse relationship between catchability (q) and stock size (N) has been reported for several marine and anadromous fishes (MacCall 1976; Peterman and Steer 1981; Crecco and Savoy 1985; Angelsen and Olsen 1987), the testing of the Paloheimo and Dickie hypothesis has been limited for most fish stocks by a lack of fisheries-independent estimates of stock abundance.

One fish species, for which there are accurate and long-term fisheries-independent population estimates, is the Georges Bank haddock, *Melanogrammus aeglefinus*, a demersal gadoid that is commercially important to the New England groundfish fishery (Clark et al. 1982; Overholtz et al. 1983). The Georges Bank haddock stock seems particularly suitable for testing the predictions of the Paloheimo and Dickie hypothesis because it has exhibited a dramatic decline during the 1970's which was thought to be mainly due to overfishing (Overholtz et al. 1986). In this paper, we used the 1964–84 commercial catch, effort, and VPA stock abundance estimates of Georges Bank haddock to test three predictions from the Paloheimo and Dickie hypothesis: (1) that q is inversely related to stock size (N) and stock area; (2) that commercial C/f is curvilinearly related to stock abundance; and (3) that the percentage of fishing effort devoted to search time is inversely related to stock abundance.

Methods

Data Source

A large amount of catch, nominal effort, and population data on Georges Bank haddock has been collected and several stock assessments are available (Rounsefell 1957; Clark et al. 1982; Overholtz et al. 1983). The United States groundfish fishery on Georges Bank uses otter trawls almost exclusively to harvest haddock (Clark and Overholtz 1979). Monthly commercial haddock landings in metric tons are available since 1931 from Georges Bank (statistical areas 521-526) (Fig. 1), and nominal fishing effort, consisting of days fished for tonnage class 3 and 4 vessels, days aboard and number of trips to each statistical area, has been collected monthly since 1964 (Clark and Overholtz 1979).

The groundfish fishery on Georges Bank is known to exploit several finfish species at the same time (Collie and Sissenwine 1983; Overholtz and Tyler 1985), so there are no straightforward methods by which to estimate directed fishing effort on Georges Bank haddock. Previous bottom trawl surveys (Overholtz 1985; Overholtz and Tyler 1985) indicated, however, that adult (age 2+) haddock tend to congregate after spawning in their preferred bottom habitat located mainly in statistical area 523 (Northeast Peak) of Georges Bank (Fig. 1). Although the geometric mean fraction of haddock landings in the mixed fishery was highly variable among the six statistical areas (Table 1), the average fraction of haddock were consistently highest in area 523. Also, the total haddock landings in area 523 were always higher than haddock landings from the other statistical areas (Clark and Overholtz 1979). As a result, we assumed that fishing effort (days fished) by the groundfish fishery within statistical area 523 was directed toward haddock. Having the annual haddock landings (C^*) and fishing effort (f^*) from area 523 from 1964 through 1984, catch per effort from area 523 was expressed as C^*/f^*. Since C^* represents a subset of the total United States haddock landings (C_{total}) on Georges Bank, total directed fishing effort data (f_{total}) were stimated (Gulland 1983) by dividing the total United States landings (C_{total}) by C^*/f^*:

$$(3)\quad f_{total} = C_{total}/(C^*/f^*),$$

which are given in Table 2. Since C^*/f^* estimates from area 523 are higher than those from other areas, the estimates of total fishing effort (f total) may be underestimated.

Relative and absolute estimates of haddock population size on Georges Bank were also made between 1964 and 1984. Virtual population analysis (VPA) was used to estimate adult (age 2+) haddock stock size in number and weight (Table 3) from 1964 through 1984 (Clark et al. 1982; Overholtz 1986). Relative abundance indices (stratified mean weight and number/tow) of adult haddock on Georges Bank were monitored during autumn (September–October) bottom trawl surveys (Table 4) by the National Marine Fisheries Service from 1964 through 1987 (Grosslein 1969; Clark 1979). We used haddock catch, effort, and population estimates from 1964 through 1984 to test the three elements of the Paloheimo and Dickie (1964) hypothesis. Since previous tagging studies (Needler 1930; Grosslein 1962; Halliday and McCracken 1970) show that Georges Bank haddock are relatively isolated from haddock stocks on Nantucket Shoals and in the Gulf of Maine, it is unlikely that recruitment and migration of haddock from nearby stocks would seriously bias the catch, effort, and VPA population estimates used in this analysis.

The relative area occupied by the haddock stock from 1964 through 1984 was estimated using the stratified mean number of adult (age 2+) haddock per tow based on the autumn trawl survey within each Georges Bank trawl stratum (strata 16, 17, 19, 20, 21, 22, and 29), and the area (km^2) of each stratum (Grosslein 1969). The stock area index (Area) in square kilometres was estimated (Table 3) by summing the stratum areas in which the arithmetic mean catch per tow of adult haddock exceeded 6.0:

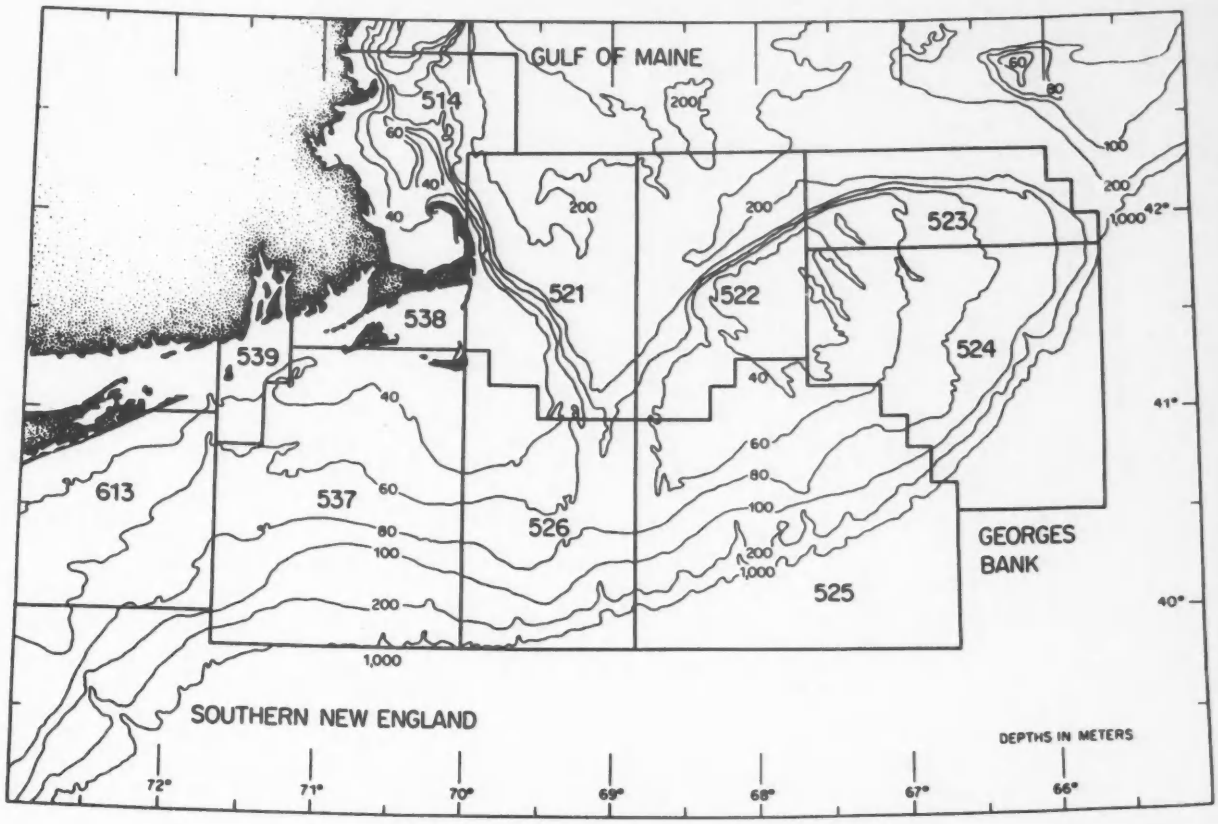

FIG. 1. Map of Georges Bank showing the location of statistical areas 521–526.

(4) $\text{Area}_i = \sum_{x_{ij}>6.0} I_j$

where x_{ij} is the stratified mean catch per tow for the ith year and the jth stratum; I_j is area (km^2) of Georges Bank comprised by the jth stratum, and the value of 6 is the overall median haddock catch per tow among all strata and years. We used median catch as a threshold value because the annual catches within strata were highly skewed with a few extremely high catches (Collie and Sissenwine 1983).

There are no direct estimates of search time by the dragger fishery on Georges Bank haddock or most other fisheries. In this study, we developed a relative index of search (days) time from 1964 through 1984 based on the total number of days fished, the total number of fishing trips, days aboard each vessel, and the approximate cruising time (days) to go back and forth from statistical area 523, where directed fishing effort on haddock is most likely to occur. The total days aboard represent the total fishing operation: (1) cruising time between port and statistical area 523; (2) days used in searching for haddock; (3) days setting and hauling the net. Of the three components, the days fished represent only the third component which is the total days needed to set and haul the net. Since it takes about 15–20 h for a commercial dragger to reach statistical area 523 from several Southern New England ports (New England Regional Fisheries Management Council 1985), we estimated the round trip cruising time to 523 to be about 1.5 d. The total cruising time each year (crus) from 1964 through 1984 was therefore the product of the total number of trips made annually at area 523 times the average cruising time per trip (1.5 d) to area 523 (Table 5). It follows that if the days fished (daf) and cruising time (crus) are subtracted from the corresponding total days aboard (tda):

(5) $\text{ser} = \text{tda} - (\text{daf} + \text{crus})$,

the remainder (ser) represents the search time expended by fishermen within statistical area 523. Search time is usually regarded as the unmeasured portion of fishing effort (Condrey 1984) which is here represented by the days fished (daf), so the relative search time (Rser) between 1964 and 1984 was expressed as a fraction of the total fishing effort (daf + ser):

(6) $\text{Rser} = \text{ser}/(\text{ser} + \text{daf})$,

which is presented in Table 5.

Empirical Test

According to the first prediction of the Paholeimo and Dickie (1964) hypothesis, the catchability coefficient (q) for most demersal and pelagic fisheries should be inversely related to fish stock abundance (N) and stock area (Area) in the form:

(7) $q = aN^B$,

and

TABLE 1. Geometric mean annual fraction of haddock over all vessel trips in the monthly finfish landings from each statistical area on Georges Bank, 1964–84.

	Statistical area				
Year	521	522	523	524	525
1964	0.55	0.69	0.78	0.43	0.53
1965	0.49	0.74	0.82	0.48	0.55
1966	0.52	0.76	0.86	0.57	0.34
1967	0.40	0.66	0.71	0.50	0.49
1968	0.44	0.50	0.72	0.34	0.35
1969	0.30	0.43	0.59	0.22	0.27
1970	0.19	0.22	0.33	0.17	0.14
1971	0.11	0.17	0.26	0.23	0.17
1972	0.11	0.13	0.24	0.13	0.06
1973	0.05	0.06	0.20	0.10	0.05
1974	0.07	0.07	0.17	0.09	0.05
1975	0.09	0.11	0.26	0.15	0.12
1976	0.11	0.10	0.15	0.10	0.08
1977	0.19	0.15	0.26	0.22	0.19
1978	0.23	0.23	0.36	0.28	0.18
1979	0.24	0.24	0.30	0.30	0.19
1980	0.23	0.28	0.43	0.32	0.25
1981	0.21	0.36	0.48	0.30	0.25
1982	0.18	0.20	0.35	0.19	0.16
1983	0.14	0.18	0.25	0.14	0.09
1984	0.11	0.16	0.23	0.18	0.14

TABLEW 2. Method of using United States haddock catch and effort data from statistical area 523 to estimate total directed fishing effort on Georges Bank haddock. The total directed fishing effort for haddock is the total United States haddock catch divided by C_{523}/f_{523}.

Year	USA haddock catch in 523 ($kg \times 10^3$)	Fishing effort in 523 (days fished) (f_{523})	C_{523}/f_{523}	Total USA haddock catch (C_{total}) ($kg \times 10^3$)	Total directed fishing effort (days fished (f_{total})
1964	7641	1586	4.82	46512	9650
1965	5537	1088	5.09	52823	10378
1966	7700	1346	5.72	52918	10396
1967	4338	930	4.66	34728	7452
1968	3051	845	3.61	25469	7055
1969	1965	549	3.58	16456	4596
1970	2414	998	2.42	8415	3471
1971	832	524	1.59	7306	4595
1972	449	377	1.19	3869	3251
1973	678	424	1.60	2777	1736
1974	159	132	1.20	2396	1997
1975	564	351	1.61	3989	2478
1976	424	371	1.14	2904	2547
1977	683	302	2.26	7934	3508
1978	1693	643	2.63	12160	4623
1979	2687	1145	2.35	14279	6076
1980	1543	547	2.82	17470	6195
1981	3035	989	3.07	19176	6246
1982	2872	1180	2.43	12567	5172
1983	2038	1021	2.00	8669	4335
1984	2784	2228	1.25	8800	7040

(8) $q = c\text{Area}^D$,

where: (*a*), (*B*), (*c*), and (*D*) are parameters to be estimated. We estimated the catchability coefficient for Georges Bank haddock (q) from 1964 through 1984 by dividing the USA haddock catches (C_{total}) in weight (kg) by the product of the VPA population size (N_{VPA}) in weight (kg) and total directed effort (f_{total}) in that year from Table 2:

(9) $q = C_{total}/(f_{total} \cdot N_{VPA})$.

To test the first prediction of the Paloheimo and Dickie (1964) hypothesis, the catchability coefficients from 1964 through

TABLE 3. Stock size from VPA (Overholtz 1986) and relative stock area for Georges Bank Haddock, 1964–84.

Year	Haddock stock size ($N \times 10^6$)	Haddock stock size ($kg \times 10^6$)	Relative stock area (km^2)
1964	248	253	10684
1965	531	428	11138
1966	279	272	10714
1967	111	144	7533
1968	65	94	3434
1969	31	58	424
1970	17	41	878
1971	14	30	424
1972	8	25	454
1973	11	17	360
1974	20	26	424
1975	19	28	2980
1976	19	34	3404
1977	100	94	878
1978	74	99	7463
1979	50	86	1675
1980	96	118	5704
1981	50	76	4218
1982	33	64	814
1983	20	46	360
1984	11	27	424

TABLE 4. Fisheries-independent estimates of relative stock size, September–November United States catches and direct effort on the stock for Georges Bank Haddock, 1964–84.

Year	Relative stock size[a] (age 2+)(kg)	Relative stock size[a] (age 2+)(*N*)	Sept.–Nov. catches ($kg \times 10^3$)	Sept.–Nov. direct fishing effort (days fished)
1964	82.2	52.3	8 659	846
1965	76.5	61.2	11 393	880
1966	24.2	17.5	10 275	846
1967	9.8	7.4	5 795	925
1968	7.6	4.9	5 545	797
1969	3.7	2.0	3 009	528
1970	6.0	2.4	1 754	375
1971	3.3	1.2	1 476	409
1972	4.0	1.4	652	217
1973	5.1	1.9	506	131
1974	3.4	1.0	371	137
1975	8.7	4.6	864	146
1976	3.7	1.7	631	136
1977	38.3	17.1	2 286	465
1978	13.3	9.1	3 031	531
1979	7.9	4.4	3 534	679
1980	29.7	13.2	3 808	548
1981	9.3	5.7	3 053	425
1982	6.1	2.9	2 490	528
1983	3.1	1.3	1 341	368
1984	3.4	1.4	1 199	436

[a]From Overholtz (1986).

TABLE 5. Estimation of relative search time (Rser) by the United States commercial fishery on Georges Bank haddock from statistical area 523, 1964–94.

Year	Days fished (daf)	Days aboard (tda)	Days cruising time[a] (crus)	Search time[b] (ser)	Relative search time[c] (Rser)
1964	1586	2198	386	612	0.278
1965	1288	1687	290	399	0.237
1966	1518	2041	359	523	0.256
1967	930	1400	239	470	0.336
1968	845	1215	213	370	0.305
1969	549	821	110	272	0.331
1970	422	644	116	222	0.345
1971	524	786	147	262	0.333
1972	377	690	119	313	0.454
1973	424	769	150	345	0.449
1974	132	266	51	134	0.504
1975	351	620	117	269	0.434
1976	371	623	107	252	0.404
1977	389	689	134	300	0.435
1978	643	1162	227	519	0.447
1979	1145	2132	395	987	0.463
1980	547	1052	213	505	0.480
1981	989	1698	354	709	0.418
1982	1180	2105	426	925	0.439
1983	1021	1700	315	679	0.399
1984	2228	3751	686	1523	0.406

[a]1.5 d times the number of fishing trips.
[b]Days aboard minus days fished.
[c]Relative search time = search time/(search time + days fished).

1984 were fitted to relative population size (*RN*) and stock area (Area) estimates (Table 3) as in equations (7) and (8) by nonlinear least squares regression analysis (SAS 1982). Linear regression analysis of the logarithmic transformed equation (7) and (8) is also possible and sometimes desirable. We, however, favored the nonlinear approach to parameter estimation because of the potential bias (Zar 1968) in back transforming the logarithmic intercept values (log a, log c) in equations (7) and (8).

Because the VPA population estimates (N_{VPA}) were used to estimate q in equation (9), it was necessary to use the survey based estimates as the independent variable in equation (7) instead of N_{VPA}. Otherwise, the statistical significance of (B) from equation (7) may be biased when N_{VPA} is contained in both sides of equation (7). If q is inversely related to haddock stock size and area, both B and D of equations (7) and (8) should be negative and differ significantly ($P<0.05$) from 0.

As for the second prediction, Paloheimo and Dickie (1964) and more recently Bannerot and Austin (1983) showed that, if equation (7) holds, then equation (2) becomes:

$$(10)\quad C/f = aN^{B+1}.$$

To test this second prediction of the Paloheimo and Dickie hypothesis for Georges Bank haddock, the 1964–84 catch per effort data (C_{total}/f_{total}) were fitted to haddock stock size (N_{VPA}) and relative stock size (*RN*):

$$(11)\quad C_{total}/f_{total} = aN_{VPA}^{B+1}$$

$$(12)\quad C_{total}/f_{total} = a_1RN^{B+1},$$

by nonlinear regression analyses. Since haddock catches (C_{total}) are used as a principal input to the VPA, it might be argued that C_{total}/f_{total} is not independent of N_{VPA} in equation (12). For this reason we tested the second prediction using both the relative population size (*RN*) and the VPA estimates as independent variables. For our data to be consistent with the second prediction, the slope ($B+1$) of equation (12) and (B_1+1) of equation (13) should be significantly ($P<0.05$) less than 1.0, indicating nonlinearity between C/f and population abundance.

An analysis of C/f versus N (equation (11)) is not only a straightforward test of the second prediction that $B+1$ is less than 1.0, but also represents an additional test on the first prediction that the catchability coefficient (q) is inversely related to $N(B<0)$. Because we considered C/f versus N (equation (11)) as the principal means by which to accept or reject the first and second elements of the Paloheimo and Dickie hypothesis, further corroboration of this relationship was made with the 1964–84 haddock relative abundance indices (*RN*) directed haddock landings ($C_{Sept.-Nov.}$) from September through November and directed fishing effort ($f_{Sept.-Nov.}$) from September through November (Table 4). The catch and effort statistics were confined to the September–November period because the NMFS autumn trawl survey was conducted in October. Directed fishing effort between September and November was estimated as in Table 2. As before, the 1964–84 C/f data were fitted to haddock relative abundance (*RN*) in a power function:

$$(13)\quad C_{Sept.-Nov.}/f_{Sept.-Nov.} = a_2RN^{B+1},$$

by nonlinear least squares methods. To confirm or refute the results from the previous analysis, we tested whether the slope (B_2+1) was significantly less than 1.0, and to what extent B_2 differed significantly from 0 as in equation (7).

For the final prediction, Paloheimo and Dickie (1964) argued that search time by commercial fishing vessels should rise as stock size declines. Searching is believed to be an important component of most fishing operations (Powles 1981), so that commercial fishermen seldom set their nets randomly on the fishing grounds. Since most pelagic and demersal fish stocks remain in schools regardless of abundance (Shaw 1978; Partridge et al. 1980), Paloheimo and Dickie (1964) concluded that a fishing vessel will search more often when stock abundance is low and confined to fewer schools.

This third prediction was tested for Georges Bank haddock as in the previous analysis by linear and nonlinear least squares regression, where the relative index of search time (Rser) (Table 5) from 1964 through 1984 was fitted to the corresponding stock size (N_{VPA}). Since Paloheimo and Dickie (1964) did not specify a particular functional relationship between search time and stock size, we fitted the search time and stock abundance data for Georges Bank haddock to linear, exponential, and power models. Our data would be consistent with the third prediction, if the slope of the regression was negative and differed significantly from 0.

Results

q Versus Stock Size and Area

The catchability coefficients (q) for the Georges Bank trawl fishery from 1964 through 1984 exhibited a significant ($P<0.05$) inverse relationship to haddock relative stock size (Fig. 2) and relative stock area (Fig. 3). The nonlinear regressions of q versus relative stock biomass and stock area (equations (7) and (8) explained 67 and 56%, respectively, of the variation in the catchability coefficient from 1964 through 1984 (Table 6). It appears that q remains relatively constant over

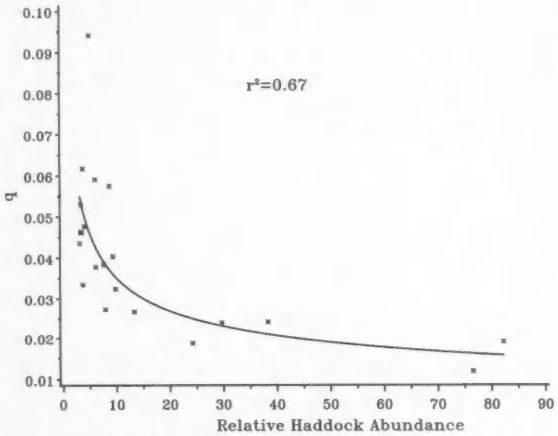

FIG. 2. Relationship between the haddock catchability coefficient (q) from the Georges Bank commercial fishery and haddock relative stock biomass, 1964–84. The solid line is the predicted relationship.

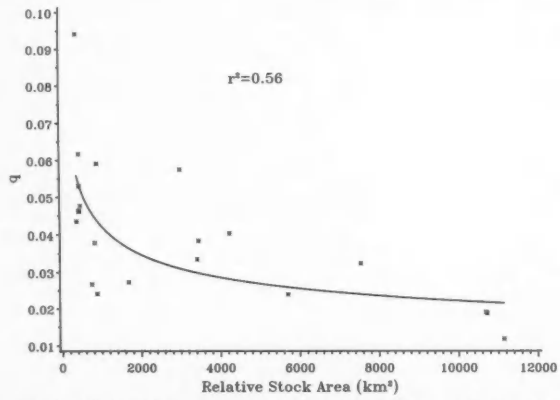

FIG. 3. Relationship between the haddock catchability coefficient (q) from the Georges Bank commercial fishery and haddock stock area (km^2). The solid line is the predicted relationship.

a wide range (15 to 85 kg/tow) of relative stock biomass, rising steadily only when haddock relative abundance fell below about 15 kg/tow.

The slope estimates (B,D) of the nonlinear regressions were significantly less than 0 (Table 6), indicating that the fishing mortality rate per unit fishing effort rises as haddock stock size and distributional range decline. An examination of the temporal variability in the catchability coefficients (q) between 1964 and 1984 (Fig. 4) indicated that q increased to the highest levels from 1969 through 1975, dropped somewhat during the late 1970's then rose again during the 1980's. This indicated that the observed inverse relationship between q and relative stock size (Fig. 2) was not due to a steady improvement in the fishing power of commercial trawlers. Note that not only was q inversely related to stock area from 1964 through 1984 (Fig. 3), but that haddock stock biomass (N_{VPA}) exhibited a positively exponential relationship ($r^2=0.74$, $P<0.001$) to stock area (Fig. 5), indicating that large haddock stocks during the mid-1960's occupied a much wider geographical area of Georges Bank. Our results suggest that haddock draggers were more efficient (higher q) at catching haddock during the early 1970's when the stock size declined below 60 thousand metric tons and was confined to a smaller geographical area on Georges Bank. These data lend support to the first part of the Paloheimo and Dickie hypotheses.

TABLE 6. Parameter estimates (a, B, D, $B+1$) from nonlinear least squares regression for the relationships between catchability and haddock relative stock size, catchability and stock area, commercial catch per effort, and stock size and relative search time and stock size from 1964 through 1984, SE = standard errors about the parameter estimaters, r refers to the approximate coefficient of determination, and P is the probability level for the approximate t-test for significance ($P<0.05$).

Parameter	Estimates	SE	r^2	Approximate t-statistic $B,D=0$ $B+1<1.0$	P
Catchability and relative stock size					
a	0.085	0.005	0.67	—	—
B	−0.384	0.062	—	6.19	<0.001
Catchability and stock area					
c	0.287	0.098	0.56	—	—
D	−0.278	0.056	—	4.96	<0.005
Catch per effort and stock size (N_{VPA})					
a	0.382	0.055	0.81	—	—
$B+1$	0.510	0.057	—	8.60	<0.001
B	−0.490	0.055	—	8.91	<0.001
Catch per effort and relative stock size					
a_1	1.142	0.423	0.52	—	—
B_1+1	0.334	0.080	—	8.33	<0.005
B	−0.665	0.169	—	3.93	<0.005
Relative search time and stock size					
e	0.444	0.0450	0.56	—	—
F	−0.0016	0.0003	—	5.33	<0.001

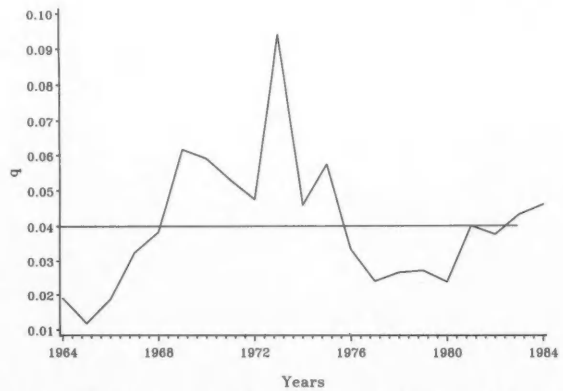

FIG. 4. Trend in the catchability coefficient (q) between 1964 and 1984. The horizontal line represents the long-term average q.

C/f and Stock Size

There were significant ($P<0.05$) curvilinear relationships between the mean annual catch per effort (C/f) and absolute and relative stock biomass (Fig. 6 and 7), and between the mean September–November C/f and relative stock size (Fig. 8) from 1964 through 1984. The coefficients of determination (r^2) for these nonlinear models (Tables 6 and 7) accounted for between 56 and 81% of the variation in C/f, whereas a simple linear

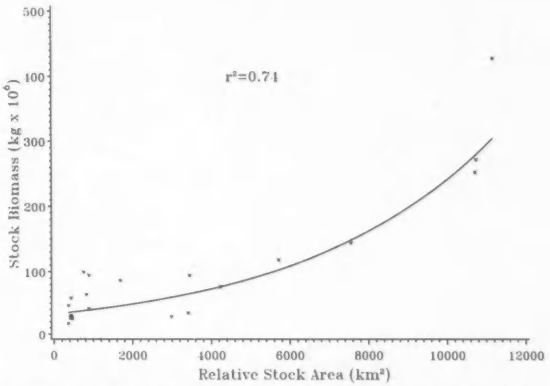

FIG. 5. Relationship between haddock stock biomass ($kg \times 10^6$) and haddock stock area (km^2) from 1964 through 1984. The solid line is the predicted relationship.

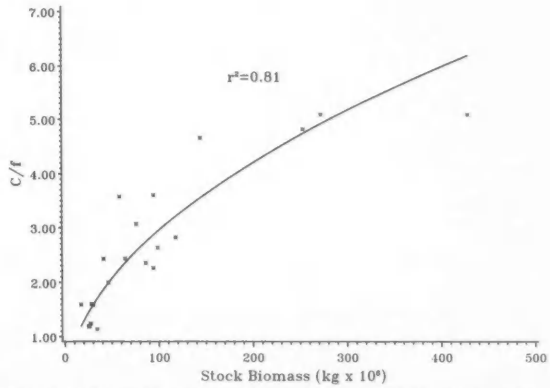

FIG. 6. Relationship between haddock commercial catch per effort (C/f) and haddock stock biomass from the VPA, 1964–84. The solid line is the predicted relationship.

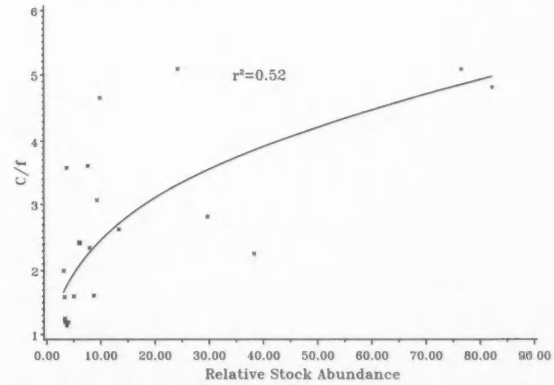

FIG. 7. Relationship between haddock commercial catch per effort (C/f) and mean relative haddock biomass (kg/tow), 1964–84. The solid line is the predicted relationship.

model could only explain about 23% of the variation. The slope estimates ($B+1$, B_1+1, B_2+1) from the three models were significantly less than 1.0 ($t=8.33$ to 11.29, $P<0.001$), with

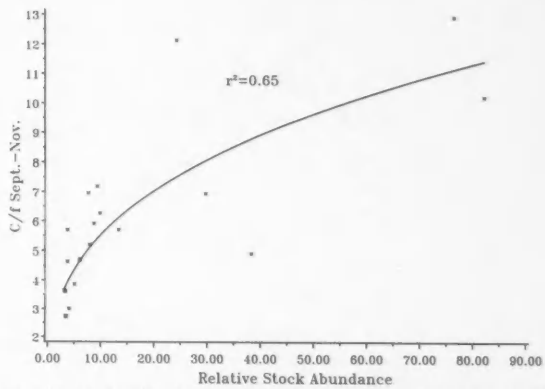

FIG. 8. Relationship between haddock commercial catch per effort from September through November and mean relative haddock biomass (kg/tow), 1964–84. The solid line is the predicted relationship.

TABLE 7. Parameter estimates (a_2, B_2, B_2+1) from nonlinear least squares regression for the relationship between Sept.–Nov. catch per effort and relative stock abundance (RN) from 1964 through 1984, SE = standard errors about the parameter estimates, r refers to the approximate coefficient of determination, and P is the probability level for the approximate t-test for significance ($P<0.05$).

Parameter	Estimates	SE	r^2	Approximate t-statistic $B=0$ $B+1<1.0$	P
a_2	2.502	0.382	0.65	—	—
B_2+1	0.345	0.058	—	11.29	<0.001
B_2	−0.655	0.099	—	6.62	<0.001

the slope estimate between C/f and N_{VPA} being significantly greater than the other two ($t=2.51$, 2.75, $P<0.05$). These data are consistent with the second prediction of the Paloheimo and Dickie hypothesis that C/f for the haddock dragger fishery on Georges Bank is curvilinearly related to stock size.

Since the slope estimates ($B+1$, B_1+1, B_2+1) for equations (12)–(14) were all significantly less than 1.0 (Tables 6 and 7), the slope (B) of equation (7) can be estimated by subtracting 1.0 from each of the $B+1$ estimates. After subtracting 1.0 from the respective slope values, the slope estimates (B) for equations (12) ($B=-0.490$, (13) ($B=-0.665$), and (14) ($B'=-0.655$) were negative and differed significantly from 0. This corroborates the first prediction from equation (7) (Table 6) that the catchability coefficient of the Georges Bank haddock fishery is inversely related to stock size.

To show more clearly how commercial catch (C) and effort (f) statistics would provide misleading haddock stock biomass and fishing mortality rates, we used our parameter estimates ($a=0.382$, $B=-0.490$) from the relationship between C/f and N_{VPA} (Table 6) to estimate fishing mortality rates (F) at two extreme levels of haddock population biomass (272 and 28 thousand metric tons) while holding directed fishing effort constant (4600 d). The instantaneous fishing mortality rate (F) in this example was estimated at the two haddock biomass levels (272 and 28 thousand metric tons) by substituting aN^{-B} for q in equation (1):

$$(15)\quad F=0.382\cdot N^{-0.490}\cdot f,$$

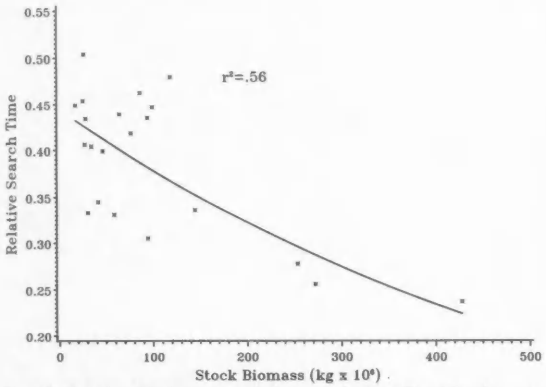

FIG. 9. Relationship between relative search time (Rser) by the commercial fishery and haddock stock biomass ($kg \times 10^6$) from 1964 through 1984. Solid line is the predicted relationship.

from which catch (C) was estimated by:

(16) $C = F \cdot N$.

At a fishing effort (f) of 4600 d and a haddock stock biomass of 272 thousand metric tons, the fishing rate (F) is 0.11 and the catch (C) is 29.9 thousand metric tons. If N declined to 28 thousand metric tons, F would rise dramatically to 0.34 even at constant fishing effort, and the catch would decline to 9.5 thousand metric tons. This indicates that a 10-fold drop in haddock stock biomass (272 to 28 thousand metric tons) results in only a 3.1-fold drop in catch (C) (29.9 to 9.5 thousand metric tons), demonstrating that commercial C/f data would seriously underestimate the true decline in haddock stock biomass. Also notice that despite constant fishing effort, the fishing mortality rate (F) would rise about three-fold (0.11 to 0.34) when biomass dropped from 272 to 28 thousand metric tons, indicating the depensatory nature of the commercial haddock fishery on Georges Bank.

Relative Search Time and Haddock Stock Biomass

There was a significant inverse relationship ($r = -0.75$, $P < 0.001$) between relative search time (Rser) and haddock stock biomass (N_{VPA}) from 1964 through 1984 (Fig. 9). The relationship was best described by an exponential model, where the slope ($F = -0.0016$) of the nonlinear regression differed significantly from 0 (Table 6). These results are consistent with the third prediction of Paloheimo and Dickie hypothesis that search time by the Georges Bank haddock fishery rises as stock biomass declines.

Discussion

The apparent negative relationship between haddock stock abundance and fishing success can be considered a depensatory density-dependent process (Clark 1974; Peterman 1977) which has important management implications. When the catchability coefficient is assumed to be consant as in the traditional theory of fishing (Baranov 1918; Beverton and Holt 1957), the exponent ($B_1 + 1$) of our equation (12) would approach 1.0, and C/f data could then be a legitimate means of monitoring proportional changes in stock abundance. However, C/f data will seriously underestimate the degree of stock decline when the exponent ($B + 1$) is significantly less than 1.0, as reported for Georges Bank haddock (Tables 6 and 7) and elsewhere (Peterman and Steer 1981; Bannerot and Austin 1983). As such, fishing mortality rates (F) are no longer proportional to changes in fishing effort (f), but are instead related to both fishing effort and stock abundance (Bannerot and Austin 1983; Angelsen and Olsen 1987). In our example for Georges Bank haddock, when stock biomass declined to low levels and q rose rapidly, a constant fishing effort generated an increasingly higher fishing mortality rate (F). Under these conditions, unless F can be restrained by a fishery closure or strict quota management (Pope 1980), spawning stock biomass would be steadily fished down, leading eventually to recruitment failure and collapse of the fishery. Given that recruitment variability is often related to climatic events (Cushing 1982), it is difficult for fisheries managers to recognize the first signs of recruitment failure when the implementation of conservation measures is most effective. As a result, fishery managers usually react slowly to early signs of recruitment failure, since even the emergence of two or three weak year-classes in succession is generally not regarded as convincing evidence of recruitment overfishing (Radovich 1979; Pope 1980), as was the case for the Georges Bank haddock (Clark 1979) and certain clupeid stocks (Murphy 1966; Clark 1974).

An inverse relationship between q and stock size and distributional area was once thought to be characteristics of schooling pelagic fishes (Fox 1974; MacCall 1976) which react to stock depletion by contracting their distributional range. However, since q was found to be negatively related to stock size for Georges Bank haddock and other demersal (Pope and Garrod 1975; Houghton and Flatman 1980; Angelson and Olsen 1987), anadromous (Peterman 1981; Peterman et al. 1985; Crecco and Savoy 1985), and freshwater (Ryder et al. 1974; Henderson et al. 1983) fishes, we agree with the conclusions of Condrey (1984) and Winters and Wheeler (1985), that depensatory fishing mortality at low stock size is a general phenomenon among most commercial fisheries.

The underlying cause(s) for the rise in catchability (q) with declining stock abundance have been attributed to improvements in fishing power of commercial vessels (Gulland 1964), and to the nonrandom search response by fishermen following changes in stock distribution and abundance (Paloheimo and Dickie 1964; Radovich 1976). Although more advanced fish-finding devices became widely used by Georges Bank draggers during the mid-1970's (Clark et al. 1982), it is doubtful that these technological improvements alone could explain the dramatic variability in q for Georges Bank haddock between 1964 and 1984. If these technological advances were the main reason, we would have expected q to rise steadily during the 1970's, and remain high thereafter following the development of new fish-finding devices. However, when the time series of q for Georges Bank haddock was examined closely (Fig. 4), it was apparent that q rose dramatically during the early 1970's and early 1980's only after haddock stock biomass fell below about 40 thousand metric tons.

We conclude that the underlying cause of the inverse relationship between q and stock size for Georges Bank haddock is more likely due to the nonrandom search behavior of commercial fishermen coupled with the ability of Georges Bank haddock to contract its geographical distribution when stock abundance declines. We found evidence, for example, that haddock stock biomass on Georges Bank declined exponentially with their distributional area (Fig. 5). These findings are con-

sistent with the conclusions of Overholtz (1985), who reported that during the mid-1970's, the depleted stock of Georges Bank haddock maintained their overall density by reducing their geographical range to the shelf-slope interface (Overholtz and Tyler 1985) located mainly on the northeast peak of Georges Bank (Fig. 1). Since commercial trawlers use their prior knowledge of haddock habitat requirements and electronic fish-finders to locate the principal concentrations of haddock on Georges Bank, fishermen seldom fish randomly with respect to the distribution of haddock, or fish independently of other trawlers. As a result, each tow of a commercial trawler removes a progressively larger fraction (higher q) of the depleted stock, resulting in the observed inverse relationship between q and stock area (Fig. 3). Under these circumstances, commercial C/f is a reliable index of haddock density but a biased index of haddock stock abundance.

The phenomenon by which Georges Bank haddock expand and contract their geographical distribution with changes in abundance (Fig. 5) has been widely reported for other fisheries (Templeman 1974; Pope and Garrod 1975; MacCall 1976; Radovich 1979; Nakashima 1988), and is consistent with the theoretical expectations of the Paloheimo and Dickie (1964) hypothesis. As pointed out by Winters and Wheeler (1985), only under the unlikely case where distributional area remains uniform, and changes in stock abundance lead to proportional changes in density, will the catchability coefficient (q) be constant and C/f be a reliable index of stock density and abundance. Because of the nonrandom search behavior of modern trawl fisheries and proportional shifts in fish abundance and area, attempts to estimate sustainable fishing rates for Georges Bank haddock would be enhanced by including a mathematical function to express the depensatory nature of the commercial fishery. Management agencies that develop strategies for rebuilding depleted stocks, such as Georges Bank haddock, should be aware of these important conclusions.

Acknowledgements

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Vertical Migration in *Daphnia galeata mendotae* (Brooks): Demographic Responses to Changes in Planktivore Abundance

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Stirling, D. G., D. J. McQueen, and M. R. S. Johannes. 1990. Vertical migration in *Daphnia galeata mendotae* (Brooks): demographic responses to changes in planktivore abundance. Can. J. Fish. Aquat. Sci. 47: 395–400.

We tested the hypothesis that changes in vertical migration patterns in *Daphnia galeata mendotae* were correlated with changes in planktivore numbers. A 4-yr data set from Lake St. George showed that during 1982, when planktivores numbered approximately 2500·ha^{-1}, adult *D. galeata mendotae* were found in the epilimnion at both midday and midnight. During 1984 and 1985, when planktivores were almost an order of magnitude more abundant, adult *D. galeata mendotae* were detected in the epilimnion only at night, and the amplitude of migration increased by a factor of two. Changes in diel population densities were associated with these interannual differences in vertical migration patterns. These results suggest that between-year differences in vertical migration patterns were strongly associated with changes in planktivore density which may have influenced the selective value of increased hypolimnetic residence time.

Nous avons tenté de vérifier l'hypothèse selon laquelle les variations des modes de migration verticale de *Daphnia galeata mendotae* étaient en corrélation avec les variations du nombre de planctonophages. Une série de données provenant du lac St-George, et portant sur quatre ans, a montré qu'au cours de l'année 1982, au moment où les planctonophages se chiffraient à environ 2500 ha^{-1}, les adultes *D. g. mendotae* s'observaient dans l'épilimnion à midi et à minuit. En 1984 et 1985, lorsque les planctonophages étaient près d'un ordre de grandeur plus abondants, les adultes *D. g. mendotae* n'étaient présents dans l'épilimnion que la nuit; de plus, l'ampleur de la migration a doublé. Les variations des densités de populations nycthémérales étaient associées à ces différences interannuelles des modes de migration verticale. Ces résultats semblent montrer que les différences interannuelles dans les modes de migration verticale étaient étroitement associées à des variations de la densité des planctonophages, ce qui aurait pu avoir une influence sur l'importance du facteur « période de séjour accrue » dans l'hypolimnion.

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The selective advantage of vertical migration in zooplankton may stem from enhanced fecundity, energetic benefits, or improved survivorship (Johnsen and Jakobsen 1987; Gabriel and Thomas 1988). Fecundity is generally increased by remaining in warm productive surface waters (Orcutt and Porter 1983; Stich and Lampert 1984) and daily vertical migration to cold hypolimnetic water may result in energetic savings, although this appears not be the the case for *Daphnia hyalina*, *Daphnia galeata* (Stich and Lampert 1984), or *Daphnia parvula* (Orcutt and Porter 1983). Alternatively, survivorship may be increased by spending a portion of the diel period in the hypolimnion (Zaret and Suffern 1976; Geller 1986). Selection for increased fecundity should reduce the amplitude of vertical migration, whereas selection for increased survivorship should increase the amplitude of vertical migration. The tradeoff between fecundity and survival may drive changes in the pattern of vertical migration.

A number of studies have suggested that vertical migration patterns vary in response to changing levels of fish production (Huntsman 1924; Zaret and Suffern 1976; Gliwicz 1986a,b), but numerical estimates for fish populations have not been available. McQueen et al. (1989) describe a small lake community where planktivore numbers changed by an order of magnitude over several years (1982–86). These changes were accompanied by the expected changes in zooplankton biomass (Shapiro 1980; Carpenter et al. 1985; McQueen et al. 1986). These data produced the opportunity for us to test the hypothesis that changes in planktivore biomass might be associated with changes in patterns of zooplankton vertical migration.

Methods

Lake St. George is a headwater kettle lake located near Toronto, Ontario, Canada on the Oak Ridge moraine. It is an eutrophic, dimictic, clinograde, two-basin lake with a maximum depth of 16 m and a surface area of approximately 10.3 ha (McQueen et al. 1988).

Estimates of water temperature and dissolved oxygen were obtained using a YSI (model 33) oxygen/temperature meter. Estimates of spectral distribution and irradiance were made using a submersible 12 channel spectroradiometer equipped

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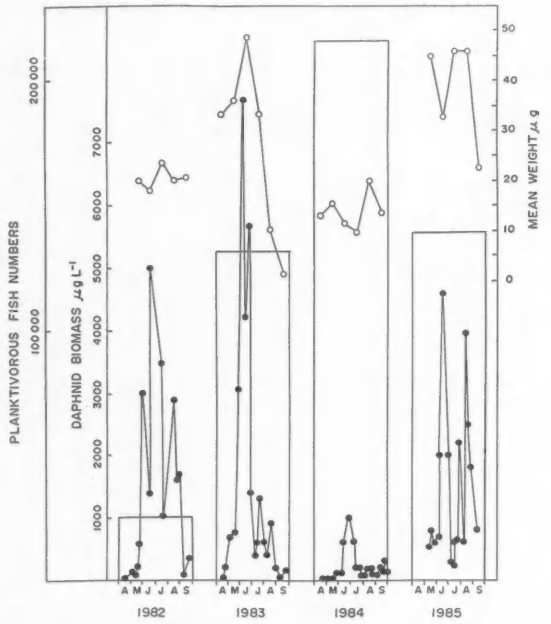

FIG. 1. Daytime biomass of daphnids (including: *Ceriodaphnin lecustris, Daphnia retrocurva, Daphnia pulex, Daphnia ambigua*, and *Daphnia galeata mendotae*) plotted with respect to years and months. The vertical bars represent estimates of total planktivore numbers at Lake St. George and the data are summarized from McQueen et al. (1988). Mean individual weights are based on measurements from all of the species listed above.

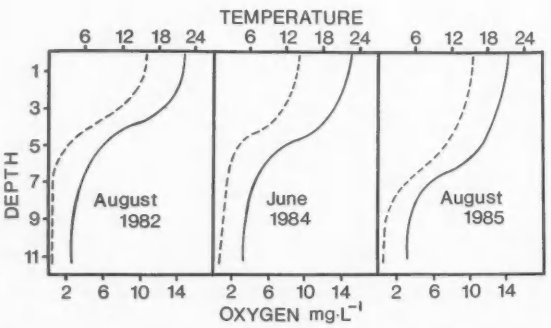

FIG. 2. Temperature (solid line) and oxygen (dashed line) values in Lake St. George on 18 August 1982, 26 June 1984, and 26 August 1985.

with 10 nm bandwidth interference filters that pass between 410 and 767 nm (MER-1000, Biospherical Instruments Inc.). Measurements of spectral irradiance at depth were made concurrently with zooplankton sampling at depth.

Sampling was performed on relatively clear, windless days. The populations were sampled in vertical series at 1-m intervals from the surface to 14 m in depth, using a 30-L, 0.5-m long, 80-μm mesh Schindler trap (Schindler 1969). Samples were preserved in a 4% formalin-sucrose solution (Prepas 1978).

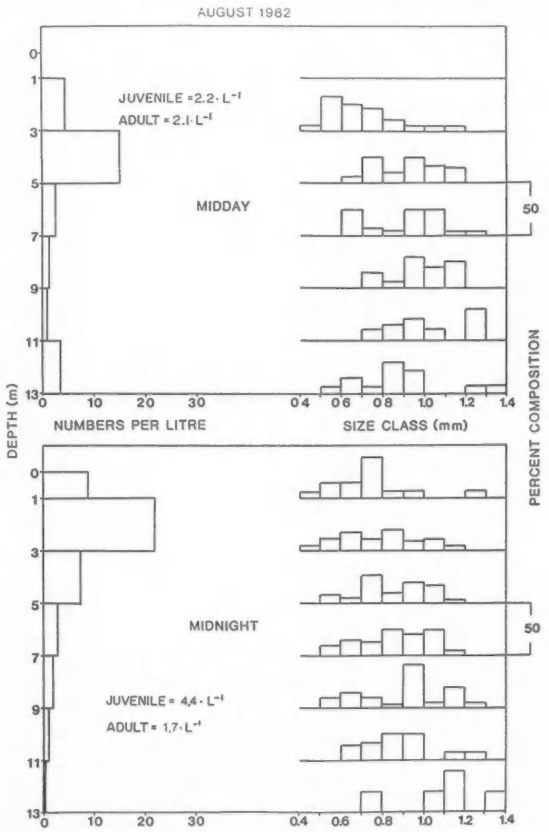

FIG. 3. Noon and midnight vertical distributions of *D. galeata mendotae* on 18 August 1982. The size-classes are in 0.1-mm intervals. The size frequency histograms indicate proportional representation in each size-class in each stratum. The density of individuals in each stratum is indicated on the left. Mean densities for juveniles and adults are shown for midday and midnight.

Sampling schedules always included both midday and midnight sampling periods.

Individual *Daphnia* were identified (Brooks 1957) and microcomputer assisted calipers (Sprules et al. 1981) were used to measure video projections of an optical image (Wild M5). The measurements were recorded and numbers per litre and size-class distributions were calculated automatically using software developed for a PET microcomputer. "Adults" were defined as individuals >0.9 mm in length (helmet to tail spine notch). "Juveniles" were <0.9 mm.

The amplitude of vertical migration was calculated as the difference between the mean population depth of a consecutive midnight and midday sampling series. Mean population depth was calculated using Tukey's trimean (Geller 1986).

D. galeata mendotae were identified, placed in 30 mL of distilled water, frozen immediately on dry ice and stored at −70°C. They were subsequently assayed at four polymorphic loci and individual genotypes were constructed by combining phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), aldehyde oxidase (AO), and amalase (AMY) phenotypes. Stain

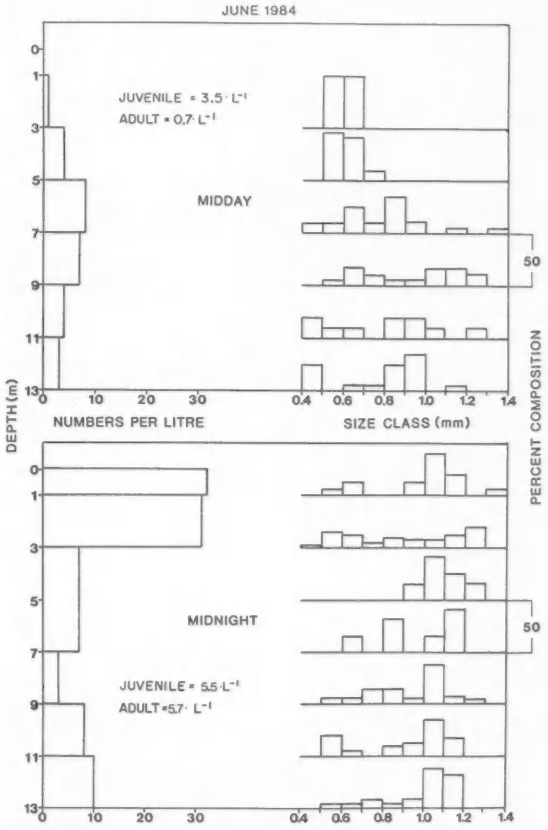

FIG. 4. Noon and midnight vertical distributions of *D. galeata mendotae* on 26 June 1984. Size-classes are in 0.1-mm intervals. The size frequency histograms indicate proportional representation in each size-class in each stratum. The density of individuals per stratum is indicated on the left. Mean densities for juveniles and adults are shown for midday and midnight.

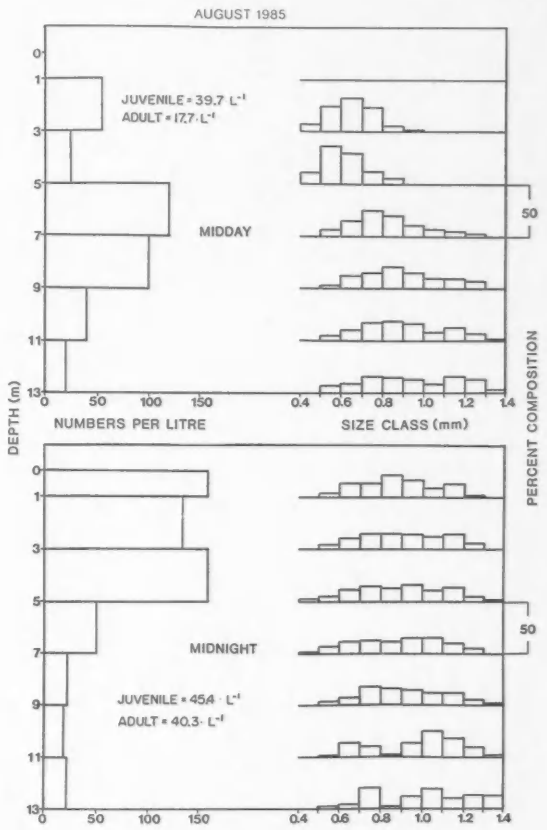

FIG. 5. Noon and midnight vertical distributions of *D. galeata mendotae* on 26 August 1985. Size-classes are in 0.1-mm intervals. The size frequency histograms indicate proportional representation in each size-class in each stratum. The density of individuals per stratum is indicated on the left. Mean densities for juveniles and adults are shown for midday and midnight.

formulas were taken from Harris and Hopkinson (1976) and Black and Krafsur (1985). Cellulose acetate gels (Helena Scientific) were presoaked in Tris-Glycine solution (3 g Trizma (Sigma), 14.4 g glycine in 1 L H_2O, pH 8). This buffer was used as both the gel and running electrolyte. Adult *D. galeata mendotae* from individual clones were ground in distilled water within sample wells and were transferred to the gel plate using an applicator (Zip Zone System, Helena Scientific). Electrophoresis was performed at 200 V for between 17 and 20 min. The stains were applied using an agar overlay.

A chi-square test for two independent samples ($\alpha = 0.05$) was used to determine the significance of differences between genotype distributions sampled at midday and midnight.

Results

A winterkill during 1981–82 reduced the piscivore and planktivore populations by >70 and >50%, respectively. The planktivores recruited rapidly in 1983 and 1984 and their populations increased to >21000·h^{-1}. Substantial piscivore recruitment was not observed until 1985 and this was associated with a reduction in planktivore numbers (McQueen et al. 1988). From 1982–85, there was an inverse relationship between planktivore numbers and both daphnid biomass (Fig. 1) and mean individual daphnid weights (Fig. 1).

There were minor between-year differences in the oxygen and temperature profiles. During 1982 and 1984, Secchi depths varied between 1–2.5 m (McQueen et al. 1988) and oxygen reductions were observed from 4 m to the bottom (Fig. 2). During 1985, the Secchi depths were greater, the epilimnion was approximately 1 m deeper and the oxygen decline began at 5–6 m.

At midday in 1982, adults were detected in the epilimnion (Fig. 3). At midday in both 1984 and 1985, adults were not detected in the epilimnion (Figs. 4, 5). The population density was about equal in 1982 and 1984, and was much larger in 1985.

At midnight all size-classes and most of the population were distributed in the epilimnion in all three years (Figs. 3, 4, 5).

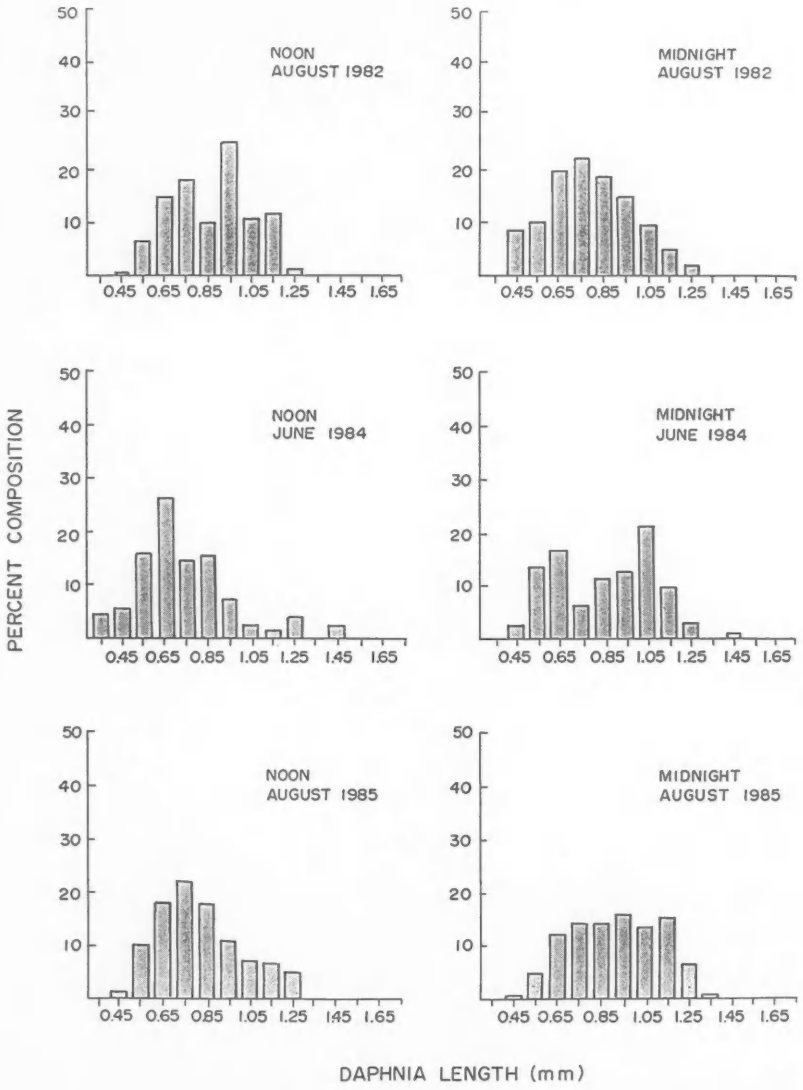

FIG. 6. Mean percent composition of *D. galeata mendotae* with respect to length (0.1-mm intervals) at midday and midnight. Adults are >0.9 mm and juveniles are <0.9 mm.

In addition, the density detected at midnight was always greater than at midday. In 1982, the midnight increase was largely due to an increase in the proportion of juveniles (Fig. 6). In 1984 and 1985 the large midnight increase was the result of a large increase in the proportion of adults (Fig. 6).

In all three years, both juveniles and adults moved vertically and the adults were always lower in the water column (Fig. 7). During 1982, the amplitude of migration was small and confined to the epilimnion. During 1984 and 1985, the amplitudes of migration were much larger and the centres of migration passed through the thermocline (Fig. 7). During 1984, critical minimum intensity of light for visual detection of *D. galeata mendotae* by golden shiners (Zaret and Suffern 1976) was at 5 m depth.

During 1985, genotypes were defined electrophoretically. Twenty-five genotypes were detected and each of five comprised >5% of the total. A particular genotype (genotype 2, Table 1) was much more abundant at midnight (chi-square $p<0.05$) and accounted for much of the increased density of adults at midnight.

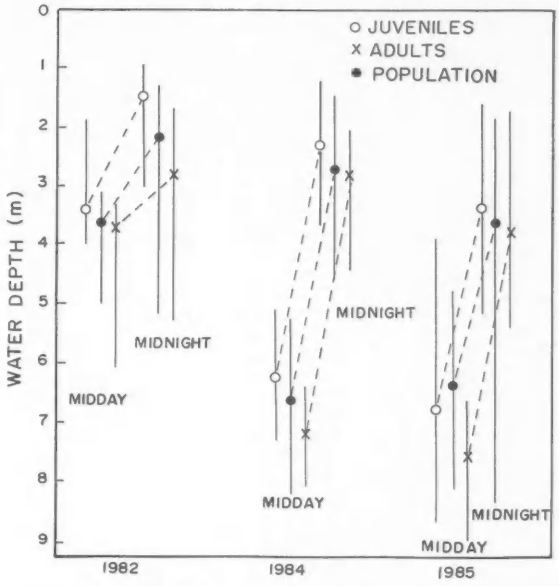

FIG. 7. Mean depths of *D. galeata mendotae* juveniles and adults (>0.9 mm) at midday and midnight during 1982, 1984, and 1985. The mean depth and ranges were calculated using Tukey's Trimean and the ranges were calculated as quartiles (Geller 1986).

Discussion

Zaret and Suffern (1976), found that on one day (July 28, 1969), in Fuller Pond, CT, USA, adult *D. galeata mendota* aggregated near 9 m during the day and moved up to 4 m around midnight. They suggested that this behaviour was a response to predation by golden shiners (*Notemigonus crysoleucas*). They also found that golden shiner feeding efficiency was greatly reduced at light levels <2200 ergs·cm^{-2}·s^{-1} which approximated the light levels found at 9 m in Fuller Pond. Finally, Zaret and Suffern (1976) reported that prior to the introduction of golden shiners in 1950, adult *D. galeata mendotae* were noted at 5 m (during 1941), although no quantitative data were available. They suggested that the distributional changes between 1941 and 1969 were related to the introduction of golden shiners.

Our data show that between 1982 and 1985 there was an overall negative correlation between planktivore density and daphnid biomass in midday samples. However, there was not a negative correlation between numbers of planktivores and numbers of *D. galeata mendotae*. For example, the large daphnid biomass observed during 1982 was only 8% *D. galeata mendotae* and mainly comprised *Ceriodaphnia* and *D. retrocurva*, whereas the large biomass observed in 1985 was 91% *D. galeata mendotae*. These results suggest that changes in species composition could not be attributed solely to vertebrate predation, but must have involved other ecological processes.

During 1982, when planktivore numbers were low (Fig. 1), adults (>0.9 mm) were found in the epilimnion at both midday and midnight (Fig. 3) and the amplitude of vertical migration was small (1.5 m) (Fig. 7). During 1984 and 1985, when planktivore densities were high, adults were seldom found in the epilimnion in midday samples (Figs. 4, 5) and the amplitude of vertical migration was large (4 m; 1984, 3 m; 1985). These results are consistent with the hypothesis (Zaret and Suffern 1976) that adult vertical migration patterns were influenced by the presence of planktivorous fish.

TABLE 1. Genotype frequencies >0.05 in Lake St. George sampled at noon and midnight in August 1985 and at noon in February 1986. The August noon and midnight samples were collected on the same date. All samples were collected at the same location.

	Genotype					Sample size
	1	2	3	9	15	
August noon	0.34	0.1	0.1	0.14	0.1	73
August midnight	0.27	0.25	0.08	0.15	0.02	182
February noon	0.28	0.31	0.09	0.09	0.04	137

In the midday samples taken in 1984 and 1985, the proportion of juveniles to adults was higher (approximately 4:1 1984, 2:1 1985) than in 1982 (approximately 1:1) (Figs. 2, 4, 5), a result that is consistent with the vertebrate predation hypothesis. However, in the midnight samples, the juvenile to adult ratios were reversed (approximately 2:1 1982, 1:1 1984, 1:1 1985). This suggests that during the high planktivore years the larger size-classes were not strongly selected against, but spent the day deep in the hypolimnion where vertebrate predation was low or nonexistent.

During 1985, the genotypic composition of the *D. galeata mendotae* population was different at midday and midnight (Table 1). This difference suggests that a portion of the midday deep hypolimnetic adult population was made up of a distinct genotypic group (genotype 2) that might have been adapted to cold water and low oxygen conditions. This suggestion is supported by the observation that genotype 2 is commonly found in the highest proportions during the winter under the ice (Stirling and McQueen 1987). Adaptations to deep hypolimnetic conditions would also favour survivorship of this group in the presence of large numbers of epilimnetic planktivores.

From the preceding analysis we conclude that the Zaret and Suffern (1976) hypothesis cannot be rejected and that interannual variations in the amplitude of vertical migration in *D. galeata mendotae* were strongly associated with the density of planktivores. We also found that the observed changes in migration patterns were accompanied by shifts in the adult to juvenile ratio between midday and midnight, and by shifts in the midday to midnight genotype ratio. This suggests that the *D. galeata mendotae* population may have adapted to changes in predator density and that at least a portion of the adaptive response resulted from selection for large adults that increased survival through increased migration amplitudes. Finally, a significant portion of the "adult" migrating group, comprised genotype 2 which has been associated (Stirling 1987) with colder water (i.e. hypolimnetic and winter conditions). We suggest that this genotype 2 might be selected when vertebrate predation forces an increase in hypolimnetic residence time.

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Comparative Population Dynamics of *Daphnia rosea* and *Holopedium gibberum* in Four Oligotrophic Lakes

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Seasonal abundance patterns of *Daphnia rosea* and *Holopedium gibberum* showed great variability over the period 1974–83 in four coastal montane lakes of British Columbia. Though the lakes differed considerably in size, depth, and history of experimental disturbance (fish introductions, fertilization, plankton harvesting), these differences apparently had much less influence on seasonal abundance patterns than did interannual variation in environmental factors shared by all the lakes. Spring rates of population increase differed strongly among years and were positively correlated between the two species. The timing and magnitude of summer population maxima also differed significantly among years, but were not correlated between the species. Adult mortality rates tended to increase through each season for both species, but showed no clear correlations either between the species or between years. Annual differences in growth and mortality rates and peak abundances were not associated with any obvious differences in environmental factors (insolation, rainfall, water temperature). There was no evidence of direct competition between the species, in terms of negative correlations in abundance. This is surprising in view of their similar life histories and feeding ecologies.

Les configurations saisonnières de l'abondance de *Daphnia rosea* et *Holopedium giberum* ont présenté une grande variabilité au cours de la période de 1974–83 dans quatre lacs de montagnes côtières de la Colombie-Britannique. Bien que ces lacs soient très différents par la taille, la profondeur et l'histoire des perturbations expérimentales (introductions de poissons, fertilisation, prélèvement du plancton), ces différences semblent avoir eu beaucoup moins d'influence sur les configurations saisonnières de l'abondance que n'en ont eu les variations interannuelles des facteurs environnementaux que connaissent tous ces lacs. Ainsi, les taux printaniers d'augmentation des populations, très différents d'une année à l'autre, étaient en corrélation pour les deux espèces. Le moment où les populations estivales atteignaient leur maximum, et l'importance de ce maximum, était également différent de manière significative d'une année à l'autre, mais ne présentait pas de corrélation entre les deux espèces. Les taux de mortalité chez les adultes avaient tendance à augmenter au cours des saisons pour les deux espèces, mais il n'y avait pas de corrélation claire ni entre les espèces, ni entre les années. Les différences annuelles des taux de croissance et de mortalité et les abondances maximales n'étaient pas associées à des différences évidentes des facteurs environnementaux (ensoleillement, précipitation, température de l'eau). Il ne semblait pas y avoir compétition directe entre les espèces, qui se serait traduit par des corrélations négatives de l'abondance. Cela nous paraît surprenant compte tenu des écologies d'alimentation semblables que présentent ces deux espèces et des histoires qu'elles ont connues.

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Seasonal patterns of planktonic cladoceran abundance may vary from year to year and among lakes, providing insight into factors that limit their abundance and about the importance of competitive interactions. It may also be important in explaining variability in freshwater fish recruitment and growth (Mills and Forney 1987). Finally, it is an important consideration in the design of large scale field experiments aimed at measuring the impacts of disturbances such as fish introductions, fertilization, and acidification by comparisons among lakes and within single lakes over time.

This paper presents abundance and birth/death rate data for *Daphnia rosea* and *Holopedium gibberum* from a 10-yr field study of four oligotrophic lakes in the University of British Columbia Research Forest, located in the coastal mountains of British Columbia. During the study these lakes were subjected to several disturbances: fish introductions (Northcote et al. 1978), fertilization (Werring 1986), and zooplankton harvesting with large nets (Krause 1984). *Daphnia rosea* and *Holopedium gibberum* were the dominant components of the summer biomass in all lakes and years, with numerically smaller and ephemeral populations of *Bosmina longirostris*, *Diaphanosoma brachyurum*, and *Ceriodaphnia quadrangula* completing the cladoceran zooplankton community. Between them, the lakes also supported populations of the calanoid copepods

Diaptomus kenai, *D. leptopus*, *D. tyrrelli*, and *D. oregonensis*. Because the calanoid species are thought to feed preferentially upon larger food particles (Hargrave and Geen 1970; McQueen 1970, Richman et al. 1980), they may be less important to the dynamics of *Daphnia* and *Holopedium* than are the interactions of the two cladocerans with one another.

Background environmental information about the lakes, the overall design of the disturbances, and general plankton responses are reviewed in Walters et al. (1987). One of the lakes is small and shallow (Placid, 1.6 ha, 7 m maximum depth), two are of intermediate size (Gwendoline, 13 ha, 27 m; Katherine, 21 ha, 29 m), and the fourth is relatively deep (Eunice, 18.2 ha, 42 m). Over the period of the study there was substantial interannual variation in solar insolation, precipitation, and water temperature regimes. In addition, while nutrient supply to all the lakes is low, logging might have resulted in transient nutrient loading in some of the lakes, particularly early in the study period. Thus intrinsic variation among lakes, as well as inter-annual variation in climatic factors and disturbances could in principle have contributed to differences in seasonal population dynamics.

This paper shows that the interannual sources of variation were much more important than intrinsic differences among lakes. Considering the similar life histories and feeding ecologies of *D. rosea* and *H. gibberum* (Allan 1973), we had expected to see negative correlations between the species due to competitive interactions; such correlations in overall abundance or in birth/death rates were not observed,and we speculate about how the species manage to coexist.

Methods

Plankton sampling and counting procedures used in the study are detailed in Walters et al. (1987). Generally, the four lakes were sampled about once every 2 wk during the ice-free period (usually mid-April to mid-December), using a metered Clarke-Bumpus net towed diagonally through several depth strata; each sample tow ran one-quater to one-half the length of the longest axis of the lake, taking a volume of around 0.8 m^3. Subsamples for counting were taken from each tow using a plankton splitter, so as to count a target number of at least 200 individuals from the dominant species. For *D. rosea* and *H. gibberum*, juveniles and adults (egg pouch present) were categorized separately, and fecundities from each sample stratum were recorded for a subsample of 10–20 adult individuals that appeared to have intact egg pouches. Free cladoceran eggs in each stratum were counted as a separate category, and allocated to the two species in proportion to their relative abundance.

Smoothed time series of abundance were obtained by fitting the log-transformed raw counts with cubic spline functions under tension. The amount of smoothing was initially chosen using Generalized Cross Validation criteria (Craven and Wahba 1979; Silverman 1985), but this method was abandoned after an examination of the interpolated series demonstrated oscillation with a period equal to twice the average sampling interval of 2 wk. (Oscillation was evaluated by measuring the distribution of distances between adjacent inflection points ($f'' = 0$) for each interpolated curve.) Since this oscillatory behavior would be induced by undamped sampling error alone, as an alternative approach we chose to iteratively apply smoothing with increasing tension until the dominant oscillation showed a period greater than four times the average sampling frequency. In order to choose a smoothing value which would be a good representation for the entire combination of lakes and years, we aggregated the distributions of each age-class of each species to select a tension parameter for that subgroup. Estimates made this way do not imply that the turning points are intrinsically restricted to time scales over 8 wk. Instead, they simply recognize that given the frequency of field sampling, we could not reliably separate this order of dynamic behavior from measurement error at shorter time scales. After fitting, an examination of residuals showed that the smoothed estimates were unbiased for densities above 30/m^2. For lower densities the smoothed estimates were negatively biased, and were discarded from further analysis.

Birth rates were estimated from the smoothed time series of egg abundance, using empirical estimates of egg development time as a function of water temperature (Bottrell 1975). Water temperature at each sampling date was taken to be the weighted mean temperature of the depth strata where adults were found, with weights being the relative density of adults in each stratum. No published estimates were found for development times of *H. gibberum*, but because Bottrell's analysis showed little variation among cladoceran species, we assumed that his average results apply to both *H. gibberum* and *D. rosea*. The proportion of eggs hatching per day, E^m_t, at water temperature T_t (°C) was estimated using Bottrell's equation

$$(1a) \quad E^m_t = 1/e^{3.69 - 0.292[\ln T_t]^2}$$

where the exponential expression gives development time in days. Then E^m_t times the smoothed estimate of total egg population E_t, was taken as the birth rate (E^m) at time t: remaining eggs were designated as immature (E^i_t). This method for estimating the fraction of eggs hatching assumes a simple uniform age distribution within the egg population, no physiological "memory" of variations in temperature over the egg development period, and no effect of factors other than temperature (e.g. maternal food supply) on development time. Given a similar function describing the maturation process of immature cladocerans (Korinek 1970; Neill 1981) and estimating the weighted developmental temperature of juveniles by the same method used for eggs, the analysis can be extended to a more elaborate population model which includes a juvenile age-class. We assumed that juvenile maturation rate for both species is approximated by

$$(1b) \quad J^m_t = 1/e^{4.69 - 0.293\,[\ln T_t]^2}.$$

Using a procedure identical to that used to assign the status of eggs, juveniles were allocated to mature (J^m_t) and immature (J^i_t) categories on the basis of equation (1b) and the smoothed time series of total juvenile population.

It could be argued that applying a simplistic temperature-driven maturation function to the juvenile stage is unwarranted. Neill (1981) and Threlkeld (1979) have shown that severe food shortage can greatly delay juvenile development; but even larger errors in equation (1) are likely due to the simplified age-structure of the egg and juvenile populations (see Seitz (1979) for a review of age-structure errors). Because it implicitly represents each life-stage by a uniform age distribution, equation (1) will overestimate the maturation rates, particularly in spring when the population is growing (relatively more "young" individuals) and development times are long (10–15 and 30–35 d for eggs and juveniles, respectively). In spring for example, if simple exponential decay (mortality = 0.05/d) is assumed for the age-distributions of eggs and juveniles, the actual maturation rates will be only 20–50% of the values estimated from equation

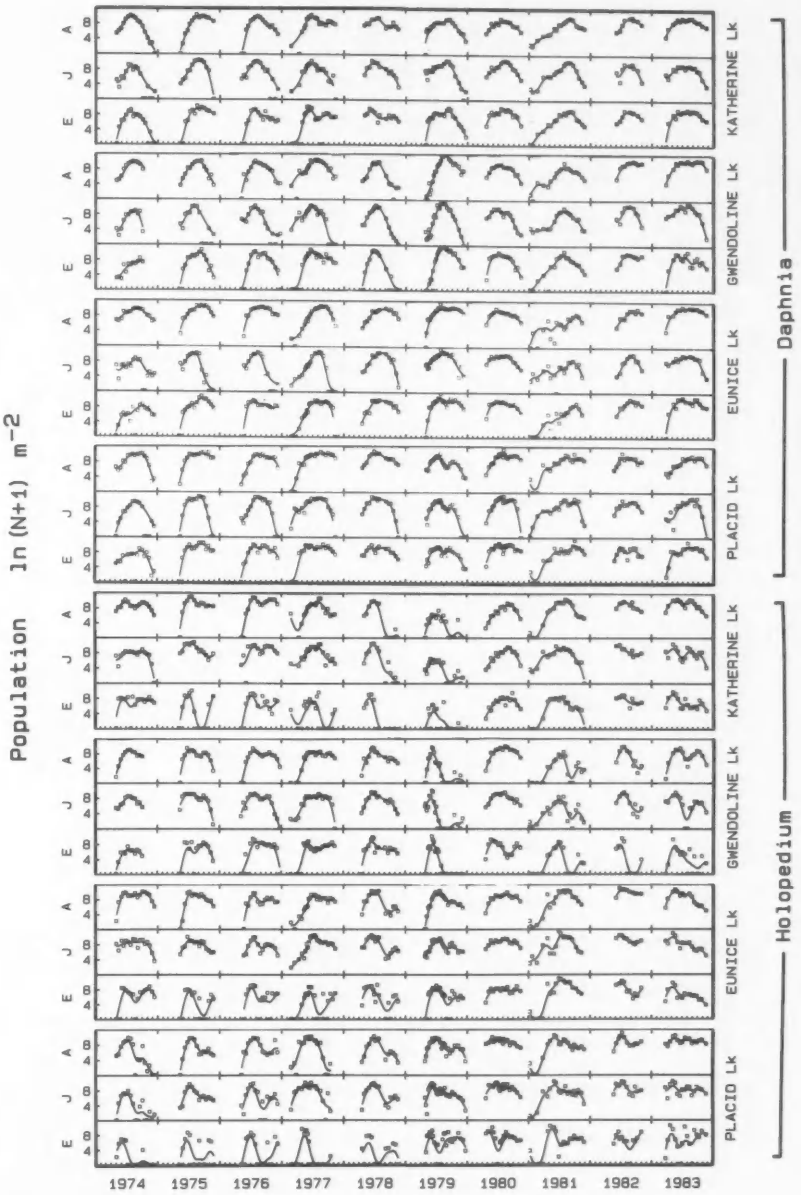

FIG. 1. Smoothed time series of numerical density of egg (E), juvenile (J) and adult (A) age-classes of *Daphnia rosea* (upper four panels) and *Holopedium gibberum* (lower four). Raw data for each sampling date are marked by open squares.

(1), depending upon the length of time required for maturation. Efforts to model the age-structure and time-lags of the egg and juvenile life-stages, and thereby account for changes in age distributions, give implausibe results because the initial age distributions of the egg and juvenile classes are not known, and because hatching of ephippial eggs (implied by apparently negative juvenile death rates) introduces new individuals to the juvenile population with no obvious age distribution.

Time series estimates of apparent mortality rates were obtained from the smoothed population estimates and egg and juvenile maturation rates given by equation (1), using a modification of an approach suggested by Argentesi et al. (1974).

Changes in the population density can be written as a set of difference equations:

$$\text{(2a)}\quad \begin{bmatrix} A & J^m & 0 \\ 0 & J^i & E^m \\ L & 0 & E^i \end{bmatrix}_t \times \begin{bmatrix} s_A \\ s_J \\ s_A \end{bmatrix}_t = \begin{bmatrix} A \\ J \\ E \end{bmatrix}_{t+1},$$

where the superscripts in the matrix indicate the immature (i) and mature (m) subcomponents of the egg (E) and juvenile (J) age-classes E_t and J_t, as estimated by equation (1). Taking the age-class estimates at time $t+1$ from the time series, the survival rates, (s) and thus mortality, can be estimated for juveniles and adults. Equation [2a] assigns $(s_A)_t$, the adult survivorship rate, to immature and newly laid (L_t) eggs. This follows from the biologically reasonable assumption that the mortality of eggs should approximate the death rate of the adults carrying them. Further inspection shows that the system of equations simplifies to:

$$\text{(2b)}\quad \begin{bmatrix} A & J^m \\ E_m & J^i \end{bmatrix}_t \times \begin{bmatrix} s_A \\ s_J \end{bmatrix}_t = \begin{bmatrix} A \\ J \end{bmatrix}_{t+1}$$

and

$$\text{(2c)}\quad L_t = [E_{t+1}/(s_A)_t] - E_t.$$

These equations are easily solved for s_t and L_t, given the smoothed time series of A_t, J_t, and E_t. One key limitation of the model is that it does not distinguish between immigration and birth, or between emigration and death. As a result, apparent death rate estimates are composite measures of all four processes. Thus the estimates can be negative, particularly at times when ephippial egg hatching is expected. By the same token they can apparently be very high when ephippial eggs fail to hatch directly to the juvenile age-class. Another limitation may lie in the assumption that the maturation functions (equation (1)) are seasonally invariant.

Key statistics of the seasonal density patterns (maximum spring rate of population increase, date of peak density, peak density) were estimated from the smoothed adult time series, and from the first derivative of those series. These measures were compared using two-way ANOVA (lakes × years) without replication (interaction effects pooled with error variance). We also attempted to develop multivariate measures of difference among the seasonal patterns, particularly in relation to the presence or absence of secondary (fall) peaks. This attempt was unsuccessful due to differences in the lengths of the series that resulted from differences in the sampling period from year to year.

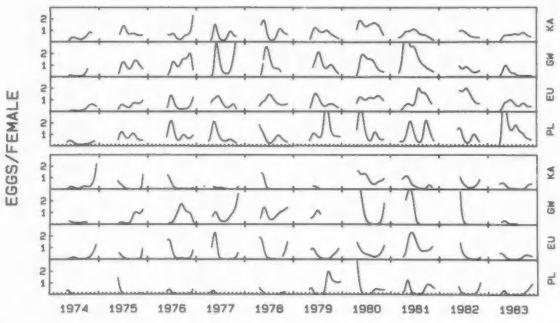

FIG. 2. Fecundity of *Daphnia* (upper panels) and *Holopedium* (lower panels), derived from the ratio of smoothed adults/eggs given in Fig. 1.

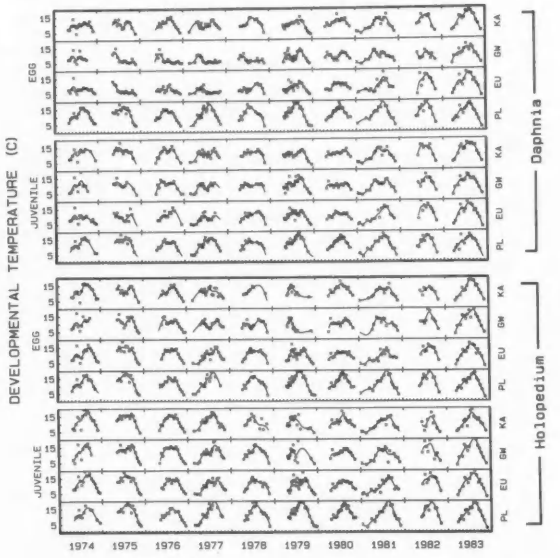

FIG. 3. Smoothed time series of mean temperature experienced by eggs and juveniles of *Daphnia* (upper two panels) and *Holopedium* (lower panels). Open squares mark the estimates of temperature, weighted by relative abundance at sampling depths, for each sampling date.

Results

The typical seasonal pattern can be described by an initial period of rapid population increase during the spring and early summer (Fig. 1), usually associated with high fecundity. This is followed by a decline in late fall, and occasionally a secondary fall peak. Declines in late fall were associated with high juvenile mortality and/or the production of resting eggs, which are presumably important in initiating subsequent spring population increases. Column-wise inspection of Fig. 1 appears to indicate strong interannual variation which is correlated among lakes. For example, spring rates of increase were relatively low for all life stages of both species in 1977 and 1981. However, care must be taken in interpreting the graphs, since the subjective visual patterns are at least partly due to differences in the duration of sampling among years.

It is remarkable that the patterns in all four lakes in Fig. 1 are so similar, considering the variety of disturbances that occurred over the study period. Introductions of cutthroat trout (*Salmo clarki clarki*) into Eunice (1975) and Gwendoline (1978–79), and of Dolly Varden char (*Salvelinus malma*) into Katherine (1974–75), were associated with decreases in mean adult body size of *D. rosea* (Northcote et al. 1978; Walters et al. 1987), but not in overall abundance. Experimental plankton harvesting in Placid during July and August, 1979, appeared to cause or exaggerate a midsummer minimum in that year, but similar harvesting in the spring of 1980 had no noticeable effect on the population development. Fertilization in Gwendoline

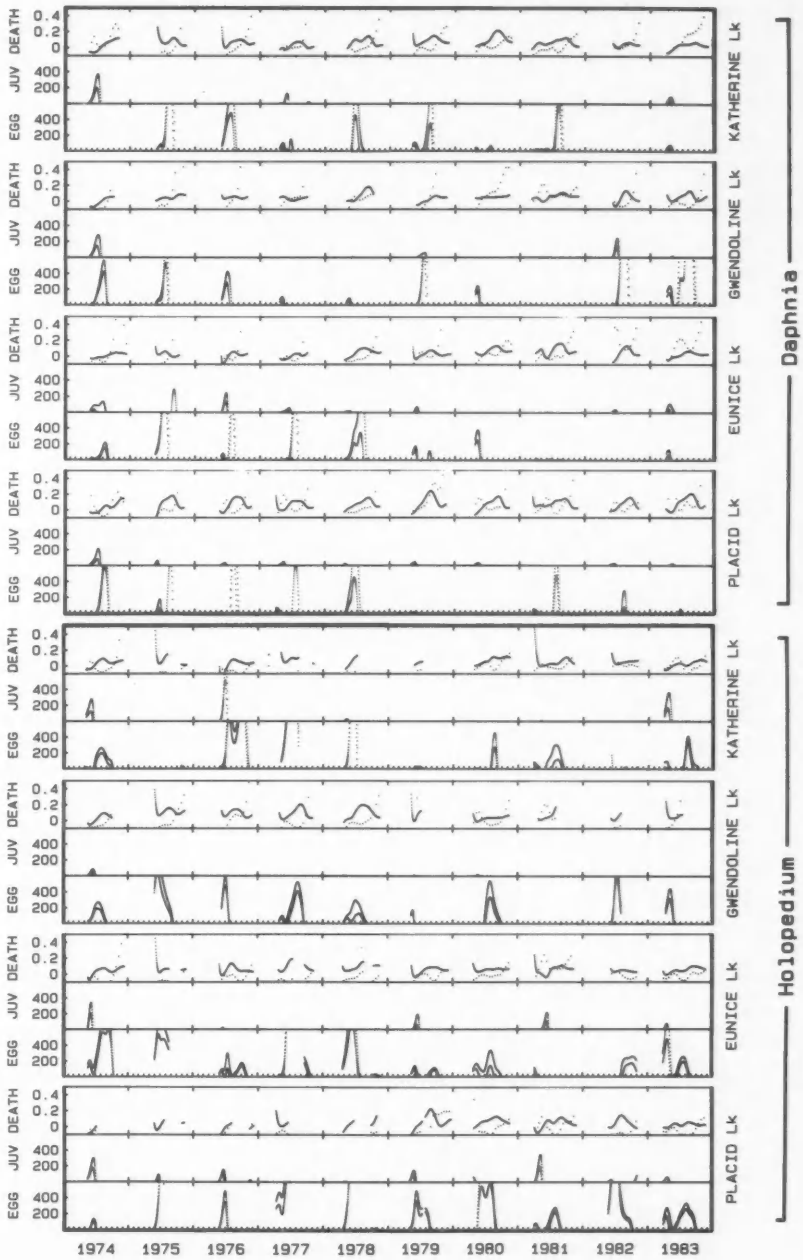

FIG. 4. Estimated apparent death rate, per day, of juveniles (dotted line) and adults (heavy line) are shown in the upper strip of each panel. The two lower strips of each panel show the rate of addition of juveniles (middle strip) and eggs (bottom strip) per square metre per day required if the actual death rates of adults and juveniles, respectively, are zero (upper line within eash strip) or 0.02/d (lower line) when the apparent death rates in that class are negative, and give an idea of the sensitivity of the negative death rate estimates to the actual population size. The upper four panels show these estimates for *Daphnia*; the lower set, for *Holopedium*. Breaks in some lines correspond to instances when the population density of any age-class fell below 30/m^2, and were excluded from analysis.

(1979) was associated with an order of magnitude increase in *Daphnia*, but one of the poorest years in the study for *Holopedium*. However, the density of *Holopedium* in Katherine was also low in that year.

Fecundity and birth rates were typically highest in spring, often showed a midsummer minimum, and often showed a secondary peak in late fall when ephippial eggs were being produced (Fig. 2). Midsummer minima were generally more pronounced for *H. gibberum*, consistent with Tessier's (1984) observation that *Holopedium* populations are vulnerable to rapid collapse, and may fall below the threshold of observation in as little as 3 d. Mean temperatures for egg and juvenile development (Fig. 3), used in the calculation of equation (1), were similar from year to year across all the lakes, in spite of substantial interannual variation in water temperature indices such as surface temperature and thermocline depth (see Walters et al. 1987 and Fig. 8).

The apparent death rates of juveniles often followed a U-shaped pattern (Fig. 4): starting high in spring but dropping quickly, followed by a slow summer rise and increasing rapidly in the fall. The apparently negative spring rates likely reflect the hatching of ephippial eggs, but might also be due to migration of juveniles from the epilimnion. The magnitudes of hatching or migration implied by these negative rates are shown in Fig. 4 as "eggs" and "juveniles," and are almost always restricted to a short period in spring. Apparent death rates of adults were less variable, and generally involved small positive values rising slowly throughout the year, sometimes with spring and fall peaks. Small fluctuations at time scales of around 2 mo are apparent in many of the computed time series. These are not clearly correlated among lakes or years, and represent residual variability not removed by the spline fitting procedure. Because the method aggregated all lakes and years within each age-class of each species to provide sufficient data upon which to base a choice for the smoothing parameter, some exceptionally noisy lake–year combinations persist in showing minor oscillations.

The comparisons which we made between the key descriptive parameters of population development — timing and magnitude of maxima, and the maximum rate of increase — are summarized in Figs. 5–7. Table 1 presents the results of two-way ANOVA comparisons of these indices. Spring rates of population increase (Fig. 5) were generally between 6–12% per day. There were significant differences in these rates among years for both species, but not among lakes. Times of peak population density (Fig. 6) also differed over years, and among lakes for *H. gibberum* due to consistently early peak times for this species in Placid. Peak population densities (Fig. 7) did not differ significantly among years, but did differ significantly among lakes for *Holopedium* due to consistently lower peaks in Gwendoline. Significant differences in population growth rate among years were due mainly to slow growth in two years (1977, 1981), whereas differences in the timing of peaks involved late peaks over two years (1980–81) near the end of the study. These years of slow growth were not unusual in terms of water temperature, thermocline formation, precipitation or insolation. However, they were preceded by warmer winters (Fig. 8; data in Walters et al. 1987). Spring population growth rates were positively correlated between *D. rosea* and *H. gibberum* (Fig. 9), whereas there were no correlations between the species in timings or magnitudes of peak population densities (Figs. 10, 11). These results suggest that the spring population growth rates of both species are limited by some common factor(s), but do not compete directly for whatever resource(s) limit maximum summer population size. For both species, slow population growth was not associated with years of relatively low spring fecundity (Fig. 2) across lakes, and there were no obvious correlations among seasonal patterns of apparent death rates.

TABLE 1. *F*-statistics and significance levels (*$P<0.05$, **$P<0.01$) for two-way ANOVA tests of differences among lakes and years in the population development measures shown in Figs. 5–7.

	Daphnia			*Holopedium*		
Source	Spring growth rate	Time peak density	Density at peak	Spring growth rate	Time peak density	Density at peak
Lake	0.94	1.88	1.38	1.50	3.75*	3.43
Year	7.50*	2.85*	1.62	29.10**	6.73*	1.43

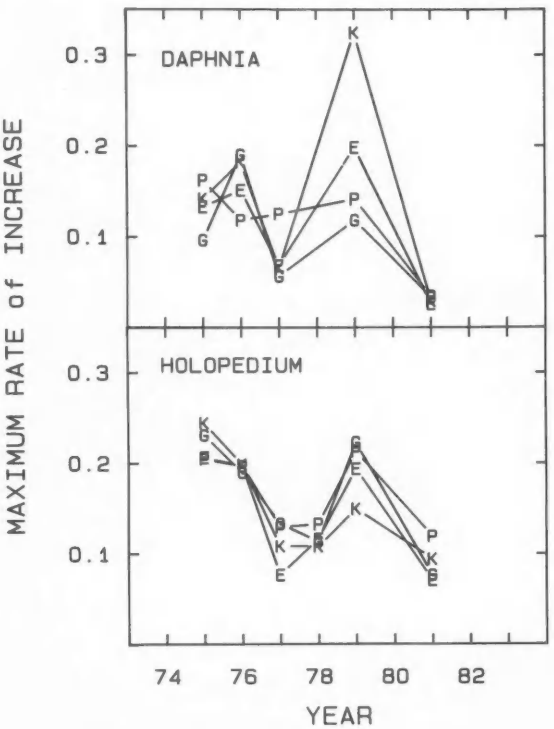

FIG. 5. Maximum rates of spring increase (per day) for *Daphnia* and *Holopedium* adults, inferred from data in Fig. 1. Data are missing for those years in which sampling began after the spring population rise was well characterized, and could not be reliably evaluated.

Discussion

In view of the many similarities in their life-histories, it is surprising that the data show no clear evidence of competitive interaction between *D. rosea* and *H. gibberum*. Both species exhibit rapid spring population growth associated with high

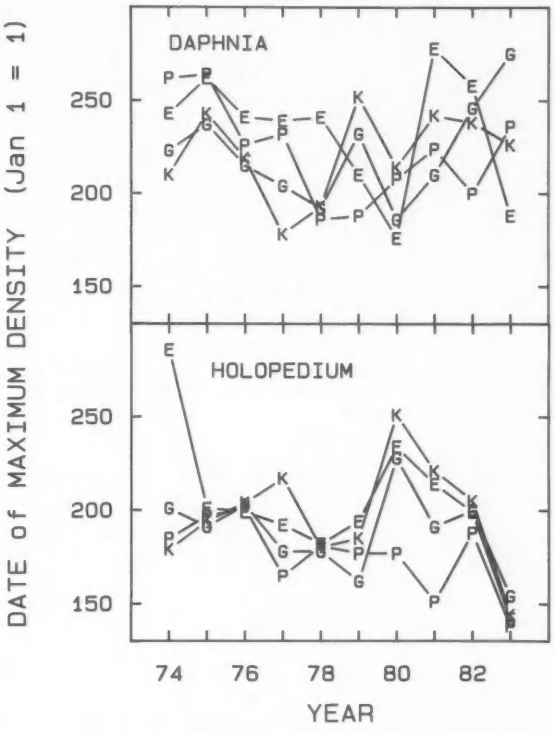

FIG. 6. Timing of maximum density of *Daphnia* and *Holopedium* adults, inferred from the data in Fig. 1.

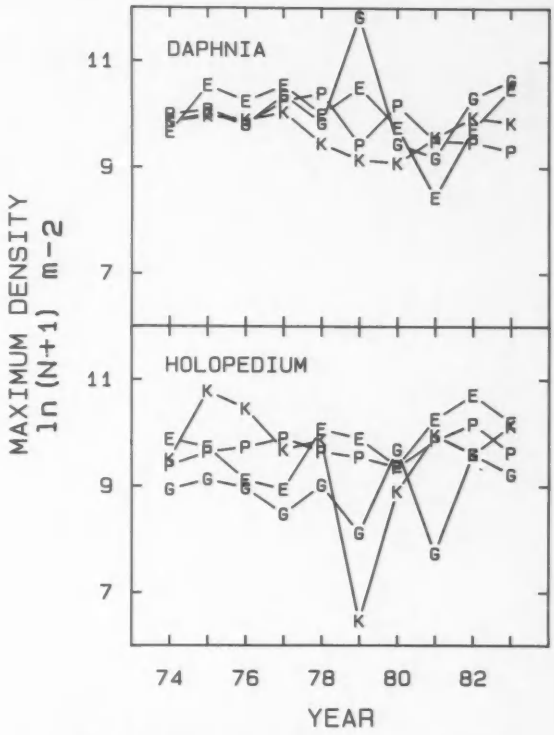

FIG. 7. Maximum density attained by adults of *Daphnia* and *Holopedium*, inferred from data in Fig. 1.

fecundity of parthenogenic females, and their emergence from resting eggs. Both show summer population peaks associated with reduced fecundity and the movement of adults into deeper water around the thermocline (data in Walters et al. 1987; Fig. 6), presumably to avoid metabolic losses associated with warm surface water. Both feed primarily on smaller phytoplankton forms (<30 μm) and have very high filtering rates (Buckingham 1978; W. E. Neill, unpubl. data). Both show fall declines associated with ephippial egg production and/or juvenile mortality, preceded in some cases by a fall burst in parthenogenic egg production. These similarities have led other authors to expect competitive tradeoffs in abundance (Allan 1973; Tessier 1986). The abundance of *Holopedium* generally peaks earlier than *Daphnia*, is less likely to show a secondary fall peak, and is more consistent in its year-to-year timing. Buckingham (1978) found that maximum feeding rate of *H. gibberum* in the Research Forest lakes is a decreasing function of water temperature over the 8–20°C range, while the maximum feeding rate of *D. rosea* increases over the same range. *Holopedium* failed to respond to summer fertilization (mid-May to mid-September) in Gwendoline Lake in 1979 or in 0.1 ha limnocorrals in Placid Lake in 1982 (Werring 1986), while *Daphnia* showed dramatic population increases following these disturbances. All these observations are consistent with the view that *Holopedium* is most successful in northern lakes because it is a low temperature "specialist." Models of competitive interactions in seasonal environments (Grenney et al. 1973; Stewart and Levin 1973; Fitzpatrick 1977) suggest that, because of an alteration in competitive advantage, such specialization may be sufficient to allow coexistence even when the species have essentially the same food type requirements: *Holopedium* being superior in spring and *Daphnia* later in the year. *Holopedium* and *Daphnia* may be viewed as the first two dominants in a seasonal "successional sequence" that involves later peaks in the abundance of *Diaphanosoma brachyurum*, *Bosmina longirostris*, and *Ceriodaphnia quadrangula*. However, during the study these other species were rarely as numerous as *D. rosea*, and never made up a large proportion of the zooplankton biomass. Although they apparently responded positively to fertilization in Gwendoline Lake in 1979 and in Placid Lake limnocorrals in 1983 (Werring 1986), their increase was less dramatic than *D. rosea*.

Patterns of apparent juvenile death rate suggest that hatching of resting eggs (inferred from negative rates) is an important component of spring population increase for both *Daphnia* and *Holopedium*. This feature becomes even more pronounced if our simple age-structure assumptions, which overestimate birth rates, are replaced by a more realistic decay process within each age-class (Taylor and Slatkin 1981). However, it is conceivable that we have substantially underestimated the total egg population, and hence birth rate, due to loss of eggs from females during sample preparation and splitting. Samples were washed and filtered one to three times through 87-μm netting, which would pass some free eggs, especially in spring when both spe-

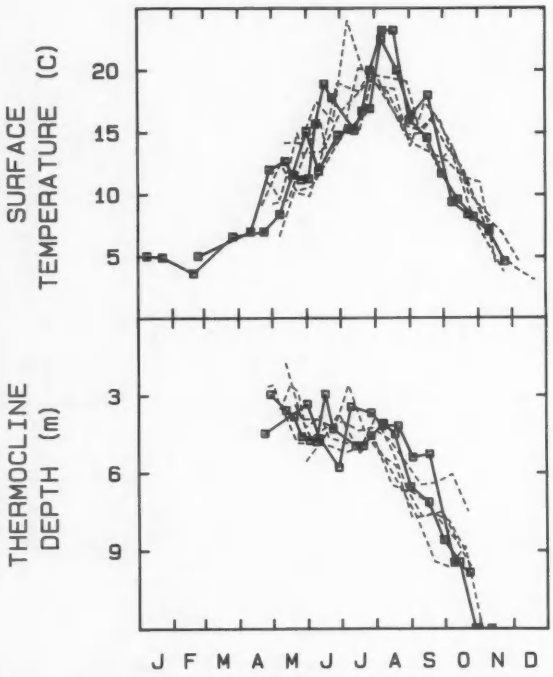

FIG. 8. Surface temperature for Katherine Lake (representative of all four lakes) is shown in the top half. The bottom half shows the location of the thermocline for sampling dates when the maximum gradient was steeper than −1°C/m. Light traces show data for the years 1975, 76, 78, 79, and 80. Heavy lines are traces of 1977 and 1981, and show that the thermal characteristics of the lakes in these two years were not remarkably different from other years.

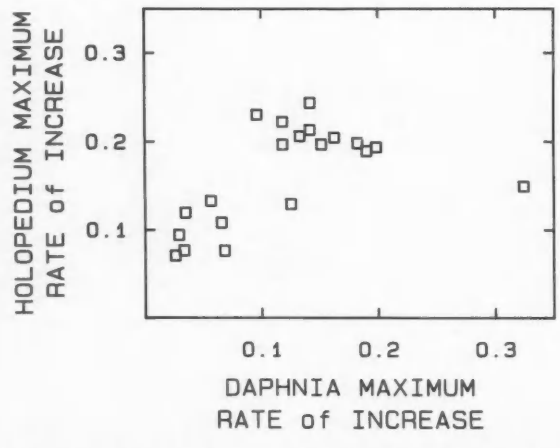

FIG. 9. Correlation of maximum rates of spring adult population increase (per day) between *Daphnia* and *Holopedium* adults, from data in Fig. 5.

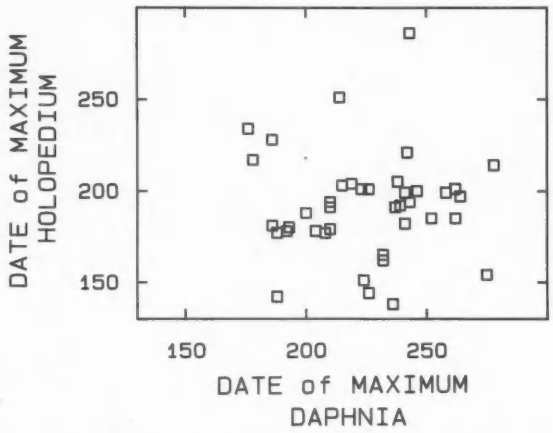

FIG. 10. Correlation of the timing of maximum density of *Daphnia* and *Holopedium* adults, from data in Fig. 6.

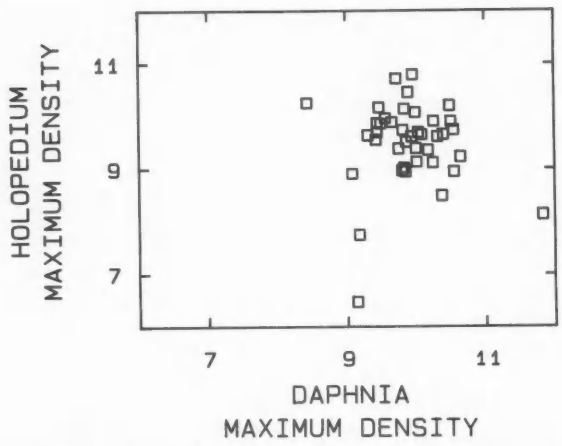

FIG. 11. Correlation of the maximum density attained by *Daphnia* and *Holopedium* adults, from data in Fig. 7.

cies tend to produce large clutches of small eggs. We have no way of correcting for this source of error, and were unsuccessful in efforts to develop anaesthetic and preservative protocols which prevent carapace deformation, and could not afford slower and more tedious sample preparation procedures which involve finer filtering of samples.

In general, we found among-year differences in population patterns to be greater than among-lake differences, but we could find no obvious environmental correlates to explain or correct for the among-year differences. Over the study period we saw substantial interannual variation in water temperature regimes (peak temperatures, thermocline depth), sunlight, and rainfall (data in Walters et al. 1987). The unusual years in terms of slow population growth (1977, 1981) were not associated with unusual patterns in any of those environmental indices. One year of late population peaking (1982) was unusually wet and cold, but the other late year (1981) was near average for the study period.

We were surprised at the lack of any clear patterns of within- or among-lake variations in seasonal rhythms of birth and death rate. We expected *Holopedium* to show higher birth and lower death rates in years of lower water temperature and shallow thermoclines (1976–78, 1980), but no such pattern is evident in Figs. 2 and 4. Likewise, we expected *Daphnia* to do better in those years, and it did not. If there are competitive interactions among the species, those interactions are not expressed in terms of any simple tradeoffs in birth and death rates. The general niche differences described by Makarewicz and Likens (1975, 1979) are certainly present in our data, but are not associated with clear differences in birth/death patterns among years for the two species. Our observations have obvious implications for design of whole-lake manipulation experiments, which are becoming increasingly popular in aquatic ecology (Schindler 1987; Carpenter et al. 1985; Carpenter 1988). They cast additional doubt on the value of temporal comparisons within single lakes (Stewart-Oaten et al. 1986), indicating instead that relatively precise comparisons should involve proper replication (Hurlburt 1984) across an experimental set of lakes.

Acknowledgments

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Experimental Lake Neutralization Program: Overview of Neutralization Studies in Ontario[1]

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(JA322)

In 1981, the Ontario Ministry of the Environment and the Ontario Ministry of Natural Resources initiated a long-term investigation of the feasibility of using neutralization to protect and rehabilitate Ontario lakes receiving high inputs of acid deposition. The objective of this inter-agency program was to provide natural resource managers with information regarding the potential utility of neutralization as a management technique, while negotiations for reductions in acidic deposition continued and control technology was developed. Neutralization is considered only a temporary measure, because it alleviates the symptoms of the problem but does not eliminate the cause. It was felt, however, that interim methods of mitigating the effects of acidification on aquatic resources should be assessed, and lake neutralization did hold promise for some situations.

The sportfish species considered most at risk from acidification in Ontario is the lake trout (*Salvelinus namaycush*) (Minns 1981). Because of the sensitivity of lake trout to acidification in Ontario and known losses of the species (Beggs and Gunn 1986), coupled with its importance as a sport fish, the study focused on assessing the feasibility of protecting or rehabilitating lake trout fisheries through neutralization. Proof of successful protection was defined as the elimination of chemical stress and restoration of effective acid buffering capacity, without inducing negative biological effects. The ultimate proof of successful rehabilitation was considered to be the restoration of a healthy, self-reproducing lake trout fishery.

While much emphasis was directed toward evaluating impacts on lake trout fisheries, it was recognized that viable ecosystems are required to support such fisheries, and that various aquatic trophic levels are adversely affected by lake acidification. Therefore, the assessment of many other biological, chemical, and physical responses of lake systems to neutralization was included in the study plan.

Intensive monitoring commenced on one fully acidified lake (Bowland Lake; 47°05′N, 80°50′W) and two lakes sensitive to acidification (Trout Lake; 45°35′N, 80°10′W; Miskokway Lake; 45°40′N, 80°14′W) in the spring of 1982. Bowland Lake had historically supported a lake trout population that had become extinct, leaving a fish community comprised solely of acid-tolerant yellow perch (*Perca flavescens*). Trout and Miskokway lakes continued to support lake trout populations as well as populations of other sportfish and forage fish species.

Bowland and Trout lakes were ultimately selected as the final candidates for neutralization. Bowland Lake was neutralized in August 1983 and Trout Lake in May 1984. Because both lakes were remote, it was most cost effective to treat them with finely powdered limestone ($CaCO_3$) dropped from a fixed wing aircraft (Molot et al. 1986).

Regular monitoring of Bowland and Trout lakes is still continuing. Monitoring of Miskokway Lake was discontinued in 1984. The results presented in this set of papers focus primarily on the responses observed in Bowland Lake. Other publications examining the Trout Lake results and additional results from Bowland Lake are planned for the future.

Findings to date have been encouraging. As described by Molot et al. (1990a), whole-lake neutralization was effective in increasing the pH and alkalinity of Bowland Lake to levels typical of dilute Precambrian Shield lakes, although even after neutralization, surface water pH depressions associated with acidic spring runoff continued. However, despite the continuance of these acid episodes, improved whole-lake water quality did allow reestablishment of a lake trout population, and ultimately, successful reproduction by the introduced lake trout, as detailed by Gunn et al. (1990).

Other aquatic trophic levels generally showed either positive responses or a lack of response to the neutralization of Bowland Lake. The phytoplankton community of the lake changed from dominance by blue-greens to dominance by other taxa, particularly chrysophytes, a more natural condition for oligotrophic Precambrian Shield lakes (Molot et al. 1990b). Aquatic macrophytes were not measurably affected by neutralization; however, profuse benthic growths of filamentous algae were rapidly eliminated, then began to reestablish very early during the reacidification of the lake (Jackson et al. 1990). These observa-

[1]The special editor for this collection of papers was Dr. P. E. K. Symons.

tions indicated that filamentous algae may be a useful, very sensitive indicator of both lake acidification and recovery.

Not all biological changes after neutralization could be directly attributed to altered chemistry. Patterns in the abundance, biomass, and size structure of zoobenthos were closely linked to changes in the fish community (Keller et al. 1990). Keller et al. (1990) also demonstrated that even after restoration of suitable water quality, recovery of natural zoobenthos community composition may be a slow process, since many acid sensitive taxa were still absent 2 yrs after neutralization.

While valuable insights have been gained on the chemical and biological effects of lake neutralization, as presented in this initial set of papers, many uncertainties remain. In particular, questions on long-term species recolonization and biological impacts during lake reacidification will be addressed during continuation of this study. Completion of the Experimental Lake Neutralization Program is scheduled for 1991.

Acknowledgements

This program was funded by the Ontario Ministries of the Environment and Natural Resources under the Acidic Precipitation in Ontario Study. Program administration and technical direction were provided by an interministerial Steering Committee and a Technical Task Force, and program coordination and report preparation were provided by B.A.R. Environmental. Many individuals made substantial contributions to this study that are not reflected in the authorships of this initial set of papers. In particular we thank T. G. Brydges, A. Burt, J. A. MacLean, B. Neary, L. Richman, W. A. Scheider, T. Stewart, F. D. Tomassini, and K. L. Yeager.

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Whole-Lake and Nearshore Water Chemistry in Bowland Lake, Before and After Treatment with $CaCO_3$[1]

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After neutralization of Bowland Lake, a clear oligotrophic acidified lake, with $CaCO_3$ in August 1983, the whole-lake pH and alkalinity increased from 4.9 and -6 $\mu eq \cdot L^{-1}$ to 6.7 and 89 $\mu eq \cdot L^{-1}$, respectively. Total whole-lake Al decreased gradually from 130 to 30 $\mu g \cdot L^{-1}$, Mn decreased from 80 to 28 $\mu g \cdot L^{-1}$ and the lake became less transparent as dissolved organic carbon (DOC) increased and Secchi depth decreased. Metals other than Al and Mn remained low and did not respond to neutralization. Between August 1983 and March 1986, about 40% of the added alkalinity of Bowland Lake was lost. Decreases of whole-lake pH following snowmelt occurred prior to but not after neutralization. Neutralization of lake water did not prevent acidic melt water from forming a distinctive acidic zone <1 m thick beneath the ice. The melt layer was more acidic than lake water, it was colder and therefore less dense, it usually contained higher Al, and it was dilute with lower conductivity and Ca. Intra-site variation was probably due to variable volumes of melt water received. A snowmelt model based on daily air temperature and precipitation predicted intermittent recharge of groundwater reservoirs during snowmelt. However, runoff was continually observed nearshore under ice suggesting that groundwater reservoirs continued to discharge after recharge ended or that the residence time of melt waters in the littoral zone was relatively long.

Le lac Bowland est un lac clair, oligotrophe, acidifié, qui a été chaulé avec $CaCO_3$ en août 1983. Après la neutralisation, le pH et l'alcalinité de l'ensemble du lac ont augmenté, passant de 4.9 et -6 $\mu eq \cdot L^{-1}$ respectivement à 6.7 et 89 $\mu eq \cdot L^{-1}$. Sur l'ensemble du lac, Al total a graduellement diminué, passant de 130 à 30 $\mu g \cdot L^{-1}$, Mn est passé de 80 à 28 $\mu g \cdot L^{-1}$, et le lac est devenu moins transparent à mesure qu'augmentait le COD et que diminuait la profondeur au disque de Secchi. Les métaux autres qu'Al et Mn sont restés en faible concentration et n'ont pas réagi à la neutralisation. Entre août 1983 et mars 1986, environ 40 % de l'alcalinité due au chaulage a disparu. Les diminutions du pH de l'ensemble du lac à la suite de la fonte des neiges, qui se produisaient avant la neutralisation, ne se sont pas produites après. La neutralisation de l'eau du lac n'a pas empêché l'eau de fonte acide de former une zone acide caractérisée de <1 m d'épaisseur sous la glace. La couche d'eau de fonte était plus acide que l'eau du lac, plus froide et donc moins dense, elle présentait généralement une concentration plus forte d'Al, et elle était diluée, avec une conductivité et une teneur en Ca plus faibles. Les variations à l'intérieur de la couche étaient probablement dues à la variabilité du volume d'eau de fonte reçu. Un modèle de la fonte basé sur la température de l'air et les précipitations quotidiennes prévoyait une alimentation intermittente des réservoirs d'eau souterraine pendant la fonte des neiges. On a toutefois observé un ruissellement continu près du rivage sous la glace, ce qui semble indiquer que les réservoirs d'eau souterraine continuaient à s'écouler après la fin de l'alimentation ou que le temps de résidence des eaux de fonte dans la zone littorale était relativement long.

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The chemical and biological effects of acidic deposition on surface waters in North America and Scandinavia are well-documented (e.g. Journal of Water, Air, and Soil Pollution, Vol. 30 and 31, 1986). Without reduction of SO_2 emissions and deposition, the neutralization of acidified waters by the addition of chemical agents can constitute both a temporary mitigative technique and an experimental tool to gauge the response of acidified systems to improvements in water quality. Improvements in water quality, however, will not necessarily result in biological restoration to a system's previous

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state, particularly if losses of important communities have occurred. Furthermore, biological differences between geographically disparate areas affected by acidification may give experimental results unique to specific areas.

The addition of $CaCO_3$ to acidified lakes leads to a significant improvement in habitat because of the resulting higher pH and alkalinity, and lower metal levels (Yan and Dillon 1984; Wright 1985). Biota adversely affected by acidic conditions that might be expected to experience beneficial effects include lake trout (*Salvelinus namaycush*) (Schindler et al. 1985), amphipods (Stephenson and Mackie 1986), *Mysis relicta* (Nero and Schindler 1983), and gastropods (Okland 1980). Whole-lake neutralization may not, however, protect biota in shallow, nearshore areas from the toxic effects of H^+ and Al during spring melt (Schofield and Trojnar 1980; Baker and Schofield 1982; Driscoll et al. 1982; Gunn and Keller 1984; Hasselrot et al. 1987).

Elevated levels of some metals such as Al and Mn are typical of acidified lakes (Dickson 1980; Dillon et al. 1984) because of increased leaching of watershed minerals and because of increased solubility in acidified waters (Stumm and Morgan 1981). Neutralization significantly reduced levels of Cu, Ni, Mn, Al, and Zn in several lakes near Sudbury, Ontario (Yan and Dillon 1984) but the levels returned to pretreatment values in Lohi Lake after the lake reacidified (the other lakes were fertilized and did not reacidify). These lakes received high atmospheric loads of metals, particularly Cu and Ni, because of their proximity to smelter emissions. In Lakes Hovvatn and Pollen, two acidified lakes in Norway, Al, Mn, and Cu decreased after neutralization while Zn, Pb, and Cd did not change and Fe increased (Wright 1985). Lindstrom et al. (1984) found that Al decreased after each $CaCO_3$ treatment and then gradually increased in three Swedish lakes neutralized repeatedly. Major ion levels, excluding Ca, are not expected to change after neutralization with a Ca-based substance (Wright 1985).

The effects of neutralization are short-lived if acid deposition rates are not reduced because of replenishment with acidic water and depletion of acid neutralizing capacity in the watershed (Dillon 1984; Sverdrup et al. 1984). Hence, reacidification rates must be monitored and decisions must be made about reneutralization to protect biota.

This study documents changes in whole-lake and episodic water chemistry resulting from the addition of calcite to Bowland Lake. The mechanics of neutralization and the short-term chemical response have been described elsewhere (Molot et al. 1986).

Study Site

Bowland Lake, a clear, oligotrophic lake 70 km north of Sudbury in northern Ontario, Canada (47°05′N, 80°50′W), is a headwater lake in a granitic basin forested mainly with black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). Surficial deposits are less than 1 m thick. The lake has a surface area of 109.4 ha, a catchment area (excluding lake surface) of 441 ha and a mean depth of 7.6 m. The maximum depth of 28 m is located in the central basin of the lake. The water replenishment time is estimated as 3 yr by assuming that annual discharge is approximately 50% of precipitation. Prior to treatment, the mean Secchi depth was 7.8 m, the pH was 4.9, the alkalinity was $-6.4\ \mu eq \cdot L^{-1}$ and total Al was approximately $130\ \mu g \cdot L^{-1}$.

Methods

Whole-lake

The study of Bowland Lake was initiated in June 1982, and $CaCO_3$ additions were made in August, 1983 (Molot et al. 1986). Samples were collected at approximately monthly intervals; however, thin lake ice during freeze-up and break-up sometimes resulted in alterations to the schedule.

Sampling was carried out in the centre of the deep basin of the lake at 2-m depth intervals using either 3-L Van Dorn or 5-L Niskin (nonmetallic) bottles. Calcium, total Al, pH, alkalinity, dissolved inorganic carbon (DIC), conductivity, pH, temperature, and dissolved oxygen (DO) were measured on samples collected from each depth. All other parameters (NO_3^-, NH_4^+, TKN, Si, total P, dissolved organic carbon (DOC), chlorophyll *a*, Na, Mg, K, SO_4, Cl, Fe, Mn, Cu, Cd, Ni, Pb, Se, and Zn) were measured on integrated samples. During periods of thermal stratification, aliquots (volume weighted) from each stratum were pooled to represent the epilimnion, metalimnion, and hypolimnion, the boundaries of which were estimated from temperature profiles. During unstratified periods, samples were pooled to represent 0 to 5 m, 5 to 10 m, and >10 m strata. These samples were pooled in clean, acid-washed, and deionized-water rinsed polyethylene carboys which were sealed tightly for transport. Aliquots were then prepared and preserved according to procedures outlined by the Ontario Ministry of the Environment (1983) for analysis of NH_4^+, NO_3^-, TKN, Si, DOC,and TP. Volume-weighted whole-lake samples were prepared for SO_4, Cl, Na, K, Mg, and metal analyses. All samples collected for metals (except Mn and Fe) analysis were preacidified in the field with 1 mL of concentrated HNO_3 per litre of sample from the beginning of the study; preacidification for Mn and Fe analyses was initiated in June 1985. A volume-weighted sample taken as twice the Secchi depth was prepared for analysis of chlorophyll *a*.

Spring melt

Sampling occurred daily during spring melt sampling periods in 1983, 1984, and 1985. Water samples were collected from mid-lake and along three transects (sites A–C) running perpendicular to shore at depths of 0, 1, and 2 m below the bottom of the ice. The transects were sampled at 0, 15, and 30 m offshore. Water samples were collected with 1- and 2-L Van Dorn bottles in 1983 and with a Nalgene vacuum hand pump and plastic tubing in 1984 and 1985.

Winter runoff patterns were simulated (Bergstrom 1975; Seip et al. 1985) to see whether climatic conditions could directly account for observed patterns in nearshore surface water quality in Bowland Lake. Only the snowmelt component of the model was used because the groundwater reservoir components could not be calibrated. The simulated runoff consisting of rainfall and snowmelt is considered to be recharge of a quickflow groundwater reservoir with a small fraction diverted into an overland flow component. Precipitation data and daily air temperatures were obtained from Environment Canada for Earlton (A), 100 km northeast of Bowland Lake. The Sudbury (A) station, although closer to Bowland Lake than Earlton (A), was typically much warmer than Bowland Lake during spring melt.

Analyses

Conductivity, pH, temperature, and DO were measured in the field. Glass reagent bottles were filled for dissolved oxygen

analysis directly from Van Dorn or Niskin bottles and fixed in the field using the azide modification of the Winkler method (APHA 1975). Dissolved oxygen concentrations were determined within 12 h of collection. pH was measured in the field within 24 h of collection using either an Orion model 811 or 701A ion meter with an Orion 91-02 pH electrode. On occasion, a portable Cole-Parmer Digisense meter with an Orion pH electrode was used. Conductivity was measured with a Lisle-Metrix C45 minibridge and temperature with a YSI 43TD telethermometer. All other analytical methods are described in Ontario Ministry of the Environment (1983).

Reacidification of a lake following treatment precludes pooling a long-term posttreatment data set in order to 'smooth', or 'eliminate' short-term (year to year) variation because pooling implies that samples are obtained from the same population. Nor can the duration of the posttreatment sampling period be lengthened in order to verify lake responses because the lake is not in a steady-state. The spectre of short-term variation as a legitimate explanation of posttreatment changes is best considered by treating several systems in different years or by the use of reference lakes (analogous to experimental controls) if suitable candidates and adequate resources exist. We have chosen to limit the posttreatment period to approximately one residence time for the purpose of pooling data in this presentation. Furthermore, the significance level for hypothesis testing was conservatively set at 1% in order to emphasize larger changes which are less likely to be due to annual variation.

Results

Whole-Lake

Major elements

The lake pH was generally uniform with depth prior to neutralization, with differences of only 0.1 between surface and bottom waters (Fig. 1). The exception to this occurred during spring snowmelt in April 1983, when acidic runoff resulted in a pH of 4.6 below the ice, while at depths >4 m the pH was 5.1–5.2. Immediately after ice-out, the less dense acidic meltwater was mixed throughout the lake. The mean lake pH was 4.6–4.7 in May and June 1983, but increased to 5.1 in July. The increase was likely caused by nutrient (NO_3^-, PO_4^{3-}) assimilation by phytoplankton during the July bloom (Molot et al. 1990) or by microbial activity in sediments. It was not due to a decrease in CO_2 because the mean lake DIC (which is virtually all H_2CO_3* at pH 5.1) increased between June and July (Fig. 1). However, alkalinity did not show the expected concomitant increase with pH. High H_2CO_3* can cause spring time pH depressions in less acidic lakes (Kratz et al. 1987).

Epilimnetic DIC values were typically less than the detection limit of 0.2 mg·L^{-1} in 1982 (measured in pooled samples) and were 0.4–0.6 mg·L^{-1} in 1983 prior to neutralization (Fig. 1). Epilimnetic values in 1984 and 1985 were 0.8–1.2 mg·L^{-1}. H_2CO_3* (calculated using temperature-dependent dissociation constants; Stumm and Morgan (1981)), was frequently below the detection limit of 17 μM during the summer of 1982 but was 28–41 μM during the summer following neutralization.

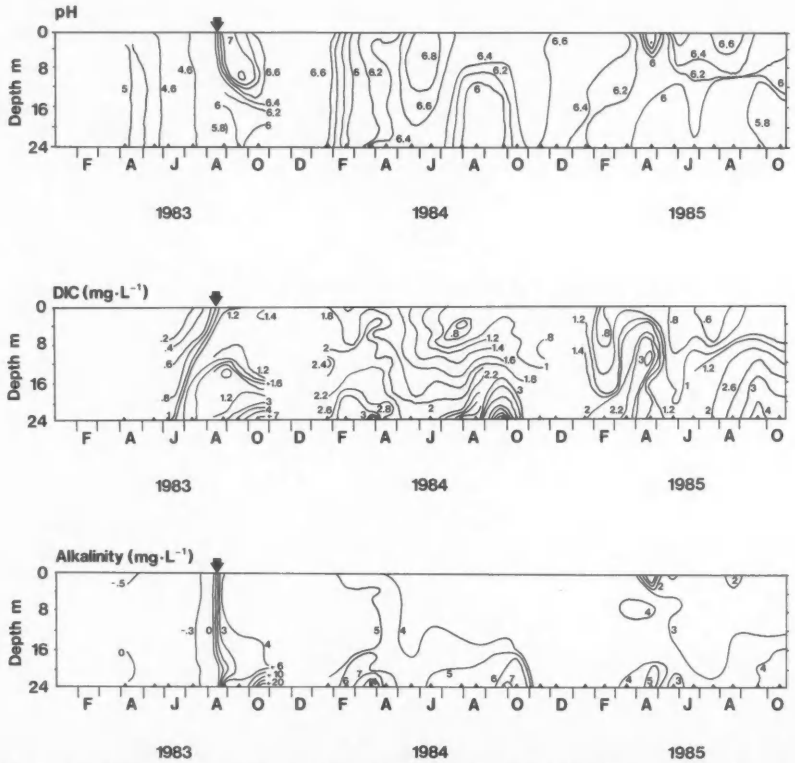


FIG. 1. pH, DIC, and alkalinity isopleths for Bowland Lake, 1983–85. The arrow indicates neutralization.

TABLE 1. (a) Ca, alkalinity, DIC, pH and DO data for Bowland Lake on March 27, 1984, and (b) calculation of contributions to alkalinity production in bottom water.

Depth (m)	Ca ($\mu eq \cdot L^{-1}$)	Alaklinity ($\mu eq \cdot L^{-1}$)	DIC (μm)	pH	DO ($mg \cdot L^{-1}$)
(a)					
0	271	101	150	6.38	—
2	254	98	133	6.43	11.34
4	249	101	167	6.42	9.12
6	247	96	150	6.32	10.08
8	251	105	175	6.24	9.92
10	252	110	167	6.26	10.40
12	244	103	167	6.33	8.64
14	253	120	200	6.17	8.03
16	258	113	208	6.15	7.53
18	259	—	208	6.16	7.79
20	261	118	208	6.13	6.50
22	266	149	242	6.11	6.06
24	384	294	417	6.63	3.20
$\bar{x}$ (2–20 m)	253	107	178		

(b)

"Recently" dissolved Ca at 24 m (originating from settled calcite) = (total Ca at 24 m − (mean Ca in water column from 2–20 m)
= 384 − 253 $\mu eq \cdot L^{-1}$
= 131 $\mu eq \cdot L^{-1}$

Alkalinity at 24 m derived from "recent" microbial activity = (total alkalinity at 24 m − (mean alkalinity in water column from 2–20 m) − (alkalinity contributed by newly dissolved calcite)
= 294 − 107 − 131 $\mu eq \cdot L^{-1}$
= 46 $\mu eq \cdot L^{-1}$

After neutralization in August 1983, pH, alkalinity, DIC (Fig. 1), and Ca increased. The postmelt whole-lake pH depression observed in May and June 1983, did not materialize in 1984 and 1985 because of entrainment of Ca-rich, high alkalinity bottom waters during turnover. Ca, which was probably derived from dissolution of calcite which settled out during neutralization, increased steadily in bottom waters during summer and winter thermal stratification. Ca build-up observed directly under-ice during early winter was probably a result of exclusion of solutes during ice formation. Dissolution of settled calcite and microbial activity were responsible for high alkalinity and DIC in bottom waters after neutralization (Fig. 1, Table 1). For example, about 16% of the total alkalinity at 24 m on March 27, 1984 was contributed by "recent" microbial activity and 45% by "recent" dissolution of settled calcite with the remainder (39%) being the background alkalinity equal to the mean water column value. Dissolution of settled calcite in the 6-mo period following treatment is consistent with the work of Sverdrup et al. (1984) who estimated that settled calcite becomes inactive after 2 yr because of surface encrustation.

Pre- and postneutralization mean values for pooled water samples are shown in Tables 2 and 3. Significant increases (*t*-test at 1% level) in NO_3^-, NH_4^+, total N, Si, and DOC were observed. The largest contributor to the increase in total N was the organic fraction, although the increase in ogranic N was not statistically significant. Higher dissolved organic matter levels could account for the increase in organic N and, therefore, total N, if dissolved organic matter had a C/N ratio by weight of 10:1. The increase in DOC may also explain the decrease in Secchi depth (Table 3) after neutralization in Bowland Lake.

In general, epilimnetic NH_4^+ increased during winter stratification and rapidly decreased following spring turnover (Fig. 2). Hypolimnetic NH_4^+ increased during winter and summer stratification. The patterns were slightly erratic because of the infrequent sampling schedule, but are probably related to mineralization of sedimented material, nitrification, and phytoplankton consumption. Epilimnetic NO_3^- increases during spring (Fig. 3) were probably due to melt water inputs. Hypolimnetic NO_3^- concentrations were relatively high in 1984 and 1985, perhaps reflecting increased rates of nitrification after neutralization (Rudd et al. 1988).

Complete dissolution of Si associated with the added calcite could account for increases of 0.02 to 0.03 $mg \cdot L^{-1}$ in the epilimnion of Bowland Lake. However, postneutralization increases were much larger than this in the middle and lower strata (Table 2). Si increases were also observed postneutralization in Lohi, Middle, and Hannah Lakes (Yan and Dillon 1984).

Significant decreases in TP were observed postneutralization (Table 2). Possible explanations include coprecipitation of PO_4^{3-} and the added Ca, and/or increased sedimentation of

TABLE 2. Means (SD, *n*) of NO_3^-, NH_4^+, total organic nitrogen (TON), total N (TN), TP, Si, DOC, and chlorophyll *a* in pooled, volume-weighted samples for pre- and postneutralization periods in Bowland Lake. Units are $\mu g \cdot L^{-1}$ for N, P, and chlorophyll *a* and $mg \cdot L^{-1}$ for Si and DOC.

	Strata Upper		Middle		Lower	
	Pre[a]	Post[b]	Pre	Post	Pre	Post
NO_3^-	27(38,17)	28[c](19,24)	15(14,17)	28[d](17,24)	22 (10,17)	38[d](18,24)
NH_4^+	10(8,17)	19[d](11,26)	9(8,17)	19[c](11,26)	22 (18,17)	31[c](25,25)
TON	132(49,17)	165[c](50,26)	125(39,17)	153[c](39,26)	133 (49,17)	152[c](35,26)
TN	169(68,17)	203[c](38,24)	149(42,17)	197[d](29,24)	176(58,17)	220[d](51,24)
TP	9(11,19)	5[c](3,76)	13(19,21)	5[c](3,76)	16(21,21)	6[c](4,72)
Si	0.52(0.34,19)	0.55[c](0.18,26)	0.47(0.16,19)	0.62[d](0.18,26)	0.59(0.16,18)	0.78[d](0.19,26)
DOC	2.0(0.4,19)	2.5[d](0.5,26)	1.9(0.4,19)	2.3[c](0.7,25)	1.7(0.3,19)	2.1[d](0.3,25)
Chl *a*	0.9(0.5,14)	1.7[c](1.6,16)	1.0 (0.7,14)	1.8[c](1.5,16)	1.6(0.6,14)	1.5[c](1.1,16)

[a]June 1982–July 1983.
[b]August 1983–October 1985.
[c]No significant postneutralization change (*t*-test at 1% level).
[d]Significant postneutralization increase (*t*-test at 1% level).
[e]Significant postneutralization decrease (*t*-test at 1% level).

TABLE 3. Mean (SD, *n*) whole-lake metal ($\mu g \cdot L^{-1}$) and major ion levels ($mg \cdot L^{-1}$) and ice-free Secchi depth (m) for pre- and postneutralization periods in Bowland Lake.

	Pre[a]	Post[b]
Fe	29–58	64–67
Cd	<0.2	<0.2
Cu	6(4,4)	3(2,8)
Ni	4(1,4)	3(1,8)
Pb	<3	<3
Se	<1	—
Zn	9(4,4)	9(7,8)
Mn	80(8,13)	28[d](23,26)
Ca[c]	2.9(0.2,15)	—
Mg	0.63(0.16,15)	0.68(0.05,26)
Na	0.71(0.12,15)	0.68(0.10,26)
K	0.40(0.10,15)	0.36(0.08,26)
SO_4	10.7(0.49,15)	10.3(0.70,25)
Cl	0.35(0.10,15)	0.30(0.17,25)
Secchi	7.8(0.4,5)	5.4[d](0.6,13)
pH[c]	4.89(0.20,6)	—
Alkalinity[c] ($\mu eq \cdot L^{-1}$)	−6.4(0.4)	—

[a]June 1982–July 1983.
[b]August 1983–October 1985, except Secchi which was May 1984–October 1985.
[c]Postneutralization Ca, pH, and alkalinity from Bowland Lake are shown in Figs. 1 and 5.
[d]Significant postneutralization decrease (*t*-test at 1% level).

phytoplankton, or more likely, contamination of early samples. Increased phytoplankton sedimentation implies increased postneutralization productivity because ice-free chlorophyll *a* levels were not significantly different. Surveys of primary production are inconclusive with regard to trends with pH (Kwiatkowski and Roff 1976; Dillon et al. 1984).

Major cations and anions other than Ca did not change significantly at the 1% level (Table 3), although the decrease in SO_4 (which is, however, significant at the 5% level) was consistent with a local decrease in atmospheric emissions in recent years (Keller and Pitblado 1986).

Metals

Of the metals measured, only Mn and Al declined significantly after neutralization (Table 3 and Fig. 4). Al declined from 130–140 $\mu g \cdot L^{-1}$ to 30 $\mu g \cdot L^{-1}$ by late 1985. Cd, Pb, Se, and sometimes Fe were below the analytical detection limit during the study period.

Temperature and oxygen

Bowland Lake is dimictic with turnover usually occurring shortly after ice-out in early May and again in mid- to late October. Ice-cover usually formed in mid-November to early December. Neutralization may have influenced the thermal regime, with hypolimnetic temperatures in July and August varying from 7.0°C in 1982 and 6.2°C in 1983 to 7.2°C in 1984 and 5.7°C in 1985. Summer surface temperatures were also cooler after neutralization, perhaps due to annual variation in climatic conditions (Table 4). However, bottom waters continued to cool in 1986 in spite of a higher number of degree-days. Lower hypolimnetic temperature is consistent with the decrease in Secchi depth (Yan 1983).

Oxygen depletion (<4 $mg \cdot L^{-1}$) usually occurred twice annually below 20 m depth. Depletion was evident by the end

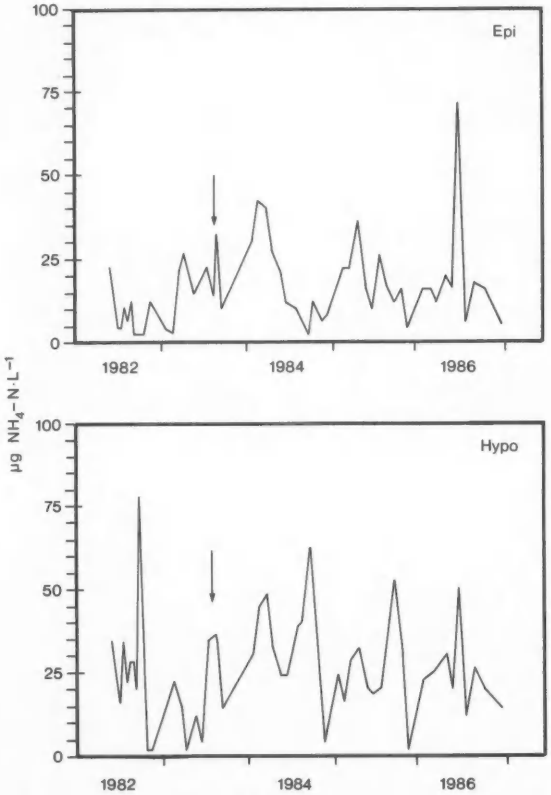


FIG. 2. Epilimnetic and hypolimnetic NH_4^+ concentrations in Bowland Lake, 1982–86. The arrow indicates neutralization.

of August and again by late March/early April and lasted until turnover both before and after neutralization.

Reacidification of Bowland Lake

Reacidification of neutralized lakes is inevitable unless the input rate of strong acid is reduced. Reacidification is expected to occur much more rapidly than initial acidification because the acid neutralizing capacity of the catchment has been depleted (Sverdrup et al. 1984). Reacidification is caused partially by direct chemical reaction of strong acid with the bases present in the lake (alkalinity) and partially by displacement of neutralized lake water with more acidic runoff water. In Bowland Lake, pH, Ca, and alkalinity decreased since neutralization (Fig. 5) with about 40% of the added alkalinity lost by March 1986.

Spring Melt

Preneutralization

During spring melt all Bowland Lake sites exhibited increased acidity (lower pH and alkalinity) and cooler temperatures (<1°C) in surface waters relative to deeper waters, while simultaneously appearing more dilute (lower total Al, DIC, and conductivity) (Fig. 6). Differences in water chemistry between 0 and 1 m depth were large while differences between 1 and 2 m were much smaller at all distances offshore.

Differences between sites were not consistent during the melt study probably because of differences in melt patterns within

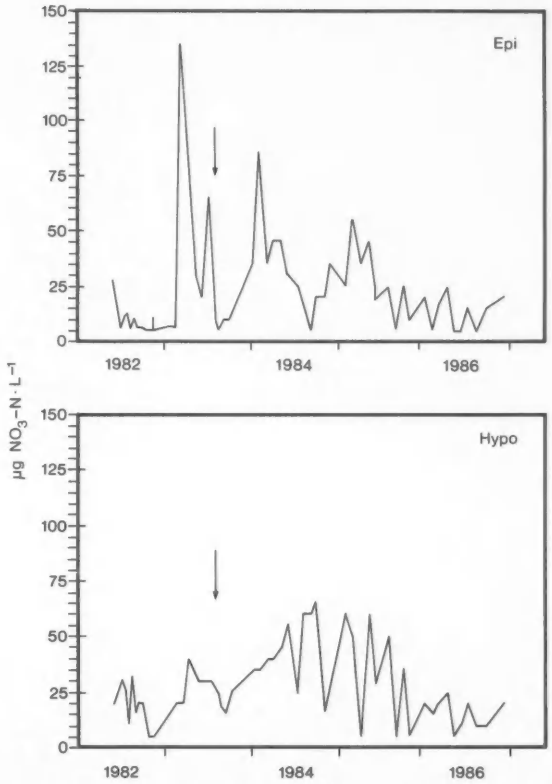


FIG. 3. Epilimnetic and hypolimnetic NO_3^- concentrations in Bowland Lake, 1982–86. The arrow indicates neutralization.

FIG. 4. Whole-lake Al and Mn concentrations in Bowland Lake, 1982–86. The arrow indicates neutralization.

the watershed. For example, Site C in Bowland Lake was more acidic and had less Al during the first 2 wk (Fig. 6), while Site A (not shown) was more acidic and periodically had less Al during the remainder of the study.

Postneutralization

The maximum daily air temperatures at Bowland Lake in 1984 were above freezing during the sampling period (March 30–April 23) except for April 6 and 7. Two major precipitation events occurred, April 6–7 and April 15–18, and were characterized by intrusions of cold water (<1°C) immediately below the ice at the sampling stations 0–30 m offshore.

As a result of the neutralization of Bowland Lake in August, 1983, lake waters were more alkaline during spring melt in 1984 (Fig. 6). Surface waters, however, became very acidic at Sites A and C during spring melt while the pH of surface waters at Site B and mid-lake was higher than Sites A and C. This suggests lower volumes of runoff at the latter sites.

If mean concentrations for 1 m depth at mid-lake are used as references representing lake water relatively unaffected by runoff, than it can be seen for Site C (Fig. 6) that (1) nearshore surface waters were relatively acidic and dilute (low conduc-

TABLE 4. Cumulative degree-days (Sudbury (A) mean daily air temperature −4°C) for the 92-d period May 1–July 31, estimated temperature at 20 m on July 31 and metalimnetic depths in Bowland Lake.

Year	Degree-days	Temperature (°C)	Metalimnion depth (m)
1982	1068	7.0	9–14
1983	1012	6.2	8–10
1984	953	7.4	6–10
1985	942	6.0	6–9
1986	1036	5.3	6–10

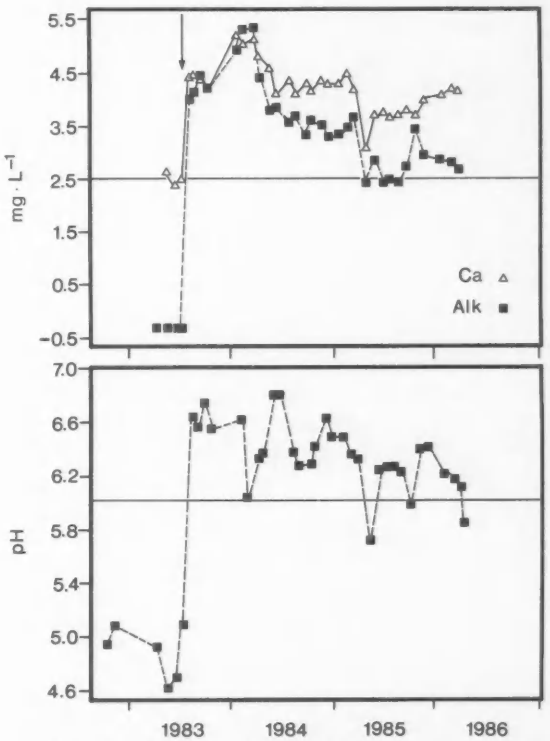


FIG. 5. Pooled, whole-lake pH, alkalinity, and Ca in Bowland Lake, 1982–86. The arrow indicates neutralization and the horizontal lines (pH 6 and 2.5 mg·L^{-1} alkalinity) are possible target levels for reneutralization.

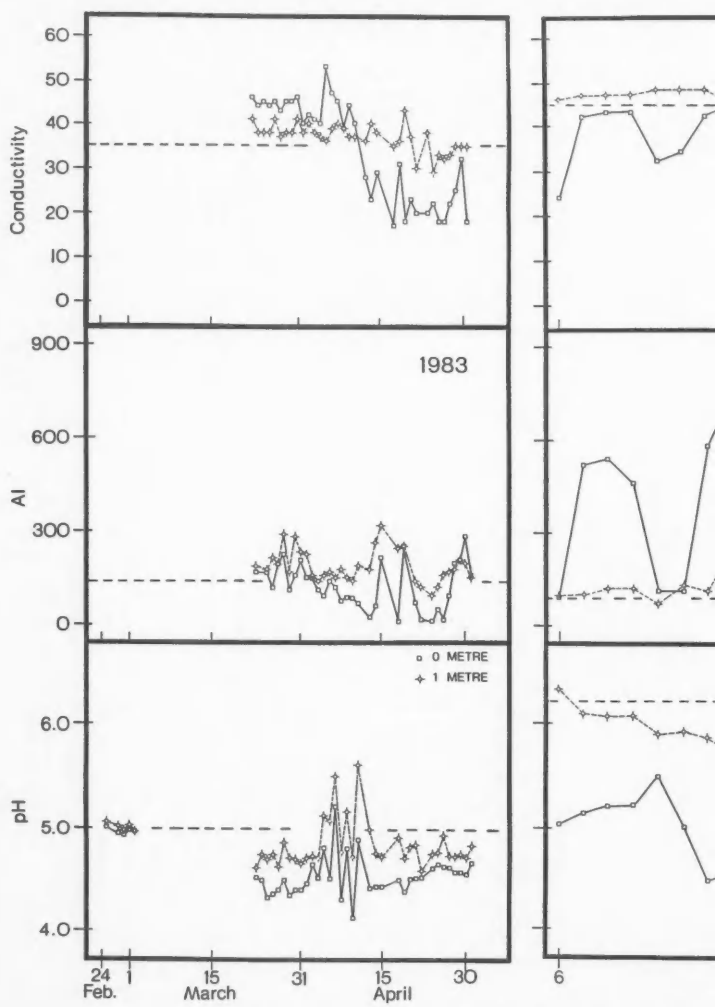
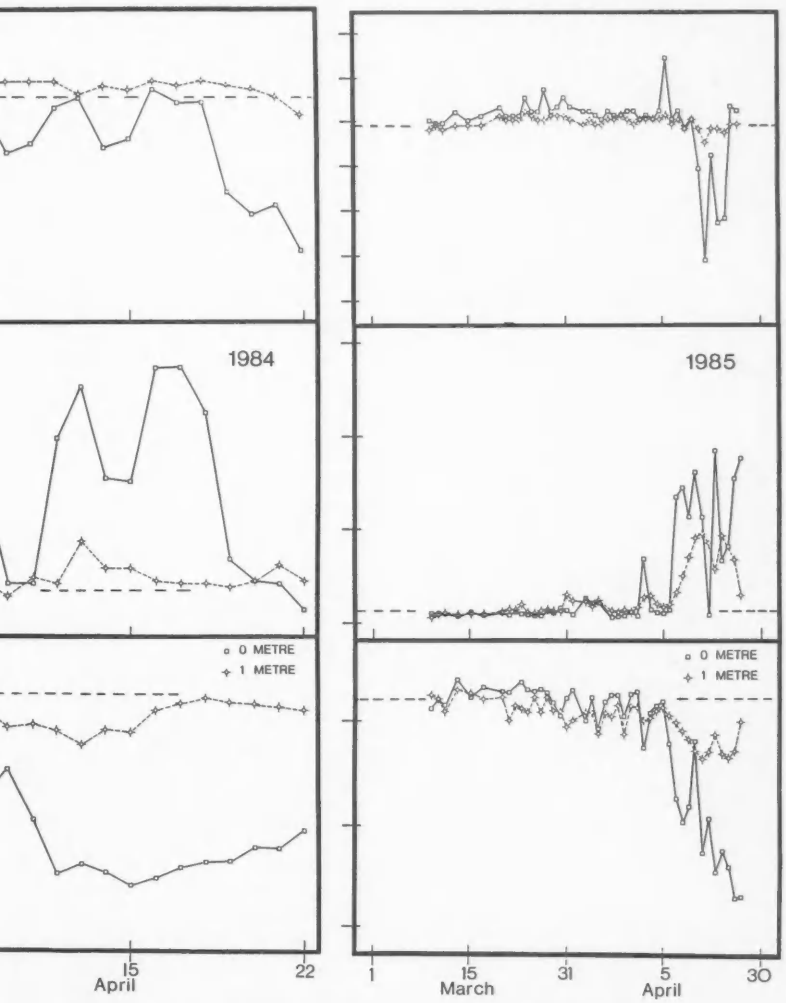


FIG. 6. pH, total Al ($\mu g \cdot L^{-1}$) and conductivity ($\mu S \cdot cm^{-1}$) during spr
m depth. The dotted lines are mean values at mid-lake at 1-m depth fo



uring spring melt in 1983, 1984, and 1985 at Site C, 15 m from shore at 0- and 1-
depth for the periods shown.

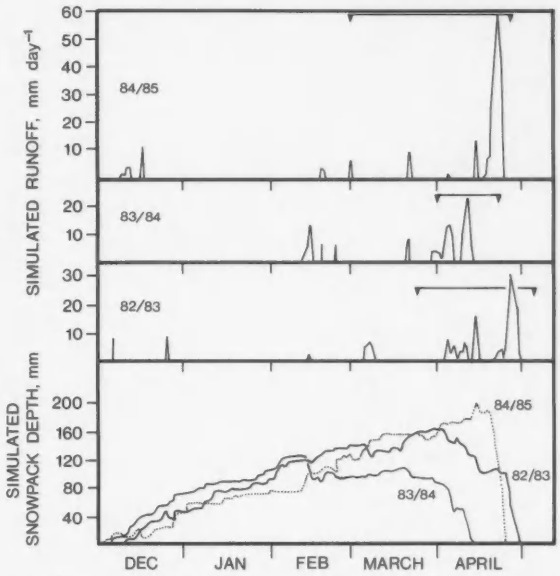


FIG. 7. Simulated daily snowpack depth and recharge (rain + snowmelt) for Earlton (A). The arrows indicate the sampling periods.

tivity) during the April sampling period in 1984, and (2) the major melt phase of April 10–20 resulted in an increase in acidity and total Al.

Comparison of mean values 15 m offshore at 0-, 1-, and 2-m depths indicates that runoff did not penetrate beyond 1 m depth in 1984. Similar results were found 30 m offshore (data not shown). Surface water chemistry did not vary with distance offshore between 0 to 30 m, but differences did occur between nearshore and mid-lake, as was also observed in 1983.

The sampling period in 1985 was the longest, lasting from March 1 until April 27 in Bowland Lake. An extended dry period occurred March 15–26. The major melt phase began about April 15 when minimum daily air temperatures increased to near freezing. As in previous years, runoff in 1985 was confined to a layer <1 m directly under the ice and was characterized by higher acidity and total Al, and lower Ca and conductivity. Mid-lake and Site B were the least affected. Ca dilution preceded the increase in total Al at Sites B and C by 7 d.

Simulation of runoff

The watershed hydrology model of Seip et al. (1985) predicted recharge (rain + snowmelt) and snowpack depth for Earlton (A) (Fig. 7). The predicted recharge and snow accumulation patterns differed during the three winters. Although major precipitation events were typically characterized by intrusions of melt water below the ice, the predicted intermittent recharge did not resemble nearshore surface water chemistry patterns which showed evidence of more continual inflow. This suggests continuing groundwater discharge into nearshore waters (Hooper et al. 1988) or relatively long residence times of discrete parcels of runoff water under ice.

Discussion

Whole-lake neutralization improved water quality conditions in Bowland Lake by significantly increasing alkalinity and reducing Al and Mn levels. The improvement in alkalinity deteriorated with time. Elevated concentrations of Mn and Al are common in acidified systems (Dickson 1980; Dillon et al. 1984) and are known to decline after neutralization, as was observed in Lake Hovvatn in Norway (Wright 1985) and Lohi, Hannah, and Nelson Lakes near Sudbury, Ontario (Yan and Dillon 1984).

Clearly, neutralization resulted in other changes in water chemistry such as increased N, Si, and DOC and decreased Secchi depth (Tables 2 and 3). Organic N increased and Secchi depth decreased in Lohi Lake following neutralization (Yan and Dillon 1984; Yan 1983); both returned to pretreatment levels following reacidification. Schindler and Turner (1982) noted a decrease in total N and an increase in transparency with acidification of Lake 223, while Kwiatkowski and Roff (1976) noted in a survey of lakes in the Killarney area, Ontario, that Secchi depth was much greater in lakes with pH <5.5. NH_4^+ and DOC increased in Lake Gardsjon after neutralization (Broberg 1987).

The probable lack of change in TP concentration in Bowland Lake is consistent with published studies which show no change in TP with neutralization (Yan and Dillon 1984; Broberg 1987) or acidification (Schindler and Turner 1982). However, mean TP concentrations decreased over a 10-yr period in acidified Lake Gardsjon in Sweden, a change attributed to increasingly efficient retention of P–Al complexes in the B-horizon of watershed soils (Janssen et al. 1986). Experimental neutralization or acidification of lakes would, of course, not alter terrestrial retention of P although internal recycling mechanisms could be affected. Studies by Mayer and Kramer (1986) and Drake and Heaney (1987) showed that P desorption increases with increasing pH, although the effect is likely to be small at low P concentrations and the resulting increase in lake TP concentration may be within experimental error.

Published data on the response of microbial communities to neutralization are inconclusive. Increased microbial activity after neutralization as measured by oxygen consumption and glucose turnover rate, has been reported by Gahnstrom et al. (1980) whereas Gahnstrom (1984) reported a short-term depression in oxygen consumption following neutralization. Counts of heterotrophic bacteria in bottom sediments decreased after neutralization in Middle Lake (Scheider et al. 1975). Sanni et al. (1983) reported slightly depressed sediment oxygen demand in Store Finnetjern in the year after neutralization. Reduced microbial activity could occur because of lower post-neutralization temperatures (Yan 1983). Kelly et al. (1984) reported that decomposition rates of freshly sedimented organic matter decreased below pH 5.25–5.0, whereas decomposition of older material was unaffected at pH values as low as 4.0. Reduced decomposition rates are consistent with low $H_2CO_3^*$ concentrations observed prior to neutralization in Bowland Lake although the pattern of oxygen depletion (<4 $mg \cdot L^{-1}$) did not change after neutralization.

Neutralization of lake water did not prevent acidic melt water from forming a distinctive acidic zone <1 m thick beneath the ice (Fig. 6). The melt layer was more acidic than lake water, it was colder and therefore less dense, it usually contained higher Al, and it was dilute with lower conductivity and Ca. Neutralization would not be expected to alter the flow and mixing of runoff under ice since these processes are likely driven by thermally controlled density differences. Henriksen and Wright (1977); Hultberg (1977); Jeffries and Semkin (1983); Charette et al. (1984); Bergmann and Welch (1985); and Gunn and Keller (1986) also found that spring melt runoff was mostly confined to a narrow layer. Variation between sites was probably due to

differences in runoff volume received and variable catchment responses to meteorological conditions.

Although Al usually increased in nearshore surface waters during pH depression episoldes, Al decreased at some sites in 1983 (including the major inlet) prior to neutralization. Reductions in Al concentrations during pH depressions suggest that there was little contact time between soils and runoff or that Al pools were depleted (Hooper and Shoemaker 1985). Runoff could also have originated from ice and snow cover on the lake (Gunn and Keller 1985). An Al decrease at 0.5 m depth in acidic Cone Lake, New Hampshire was apparently due to ice and snow melt rather than runoff because Al did not decrease in the inlet or outlet (Baird et al. 1987). Driscoll et al. (1980); Schofield and Trojnar (1980); LaZerte (1982); Sharpe et al. (1983, 1987) and Gunn and Keller (1984) found that elevated levels of total and inorganic monomeric Al coincided with decreased pH during runoff.

Only very shallow areas are likely to be affected by spring melt in Bowland Lake because of the very shallow penetration of runoff. This suggests that the decline of sensitive invertebrates and recruitment failure of lake trout in acidified lakes with very shallow penetration of runoff are caused primarily by gradual acidification of lake waters or by postmelt mixing of acidic water rather than episodic events during ice-cover (Hamilton et al. 1990). Episodic events could have a negative effect in lakes with deeper penetration (i.e. in lakes with relatively large runoff volumes or higher flushing rates).

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Response of Phytoplankton in Acidic Lakes in Ontario to Whole-Lake Neutralization[1]

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Changes in phytoplankton community composition were examined in two acidic lakes in Ontario, Bowland and Trout Lakes, to determine whether neutralization (and subsequent stocking with lake trout (*Salvelinus namaycush*) in the case of Bowland Lake) would reverse acidic characteristics. Miskokway Lake was monitored as an untreated reference lake. Analysis of community percentage similarity showed that year-to-year variability in phytoplankton community structure would have been low in the absence of neutralization. While changes in phytoplankton biovolumes or chlorophyll *a* concentrations after neutralization were not significant, there were several taxonomic changes: (1) the shift in the Bowland Lake phytoplankton community away from dominance by the cyanophyte, *Rhabdoderma*, and (2) the dominance of the prymnesiophyte *Chrysochromulina breviturrita* in the Bowland Lake phytoplankton community in 1985 2 yr after neutralization. It is likely that the major phytoplankton taxonomic changes were direct responses to chemical changes. These results suggest that structural changes (taxonomic) maintained stability of the phytoplankton communities under chemical stress (in terms of standing crop).

Nous avons examiné les modifications de la composition de la communauté phytoplanctonique dans deux lacs acides de l'Ontario, les lacs Bowland et Trout, afin de déterminer si la neutralisation (suivie d'un ensemencement de touladi, *Salvelinus namaycush*, dans le cas du lac Bowland) pouvait renverser les caractéristiques liées à l'acidification. Le lac Miskokway, non traité, a servi de lac témoin. L'analyse du pourcentage de similarité des communautés a montré que la variabilité annuelle de la structure de la communauté phytoplanctonique aurait été faible en l'absence de neutralisation. Si les changements dans les biovolumes du phytoplancton et les concentrations de chlorophylle *a* après neutralisation n'étaient pas significatifs, on a observé plusieurs modifications d'ordre taxinomique : (1) disparition dans la communauté phytoplanctonique du lac Bowland de la dominance du cyanophyte *Rhabdoderma*, et (2) dominance du prymnésiophyte *Chrysochromulina breviturrita* dans cette même communauté en 1985, deux ans après la neutralisation. Il est vraisemblable que les grandes modifications taxinomiques étaient directement en rapport avec les changements d'ordre chimique. Ces résultats semblent indiquer que les changements structuraux (taxinomiques) maintenaient la stabilité des communautés phytoplanctoniques (en terme de biomasse) sous stress chimique.

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Changes in phytoplankton species composition in acidified lakes have been well documented (Almer et al. 1974; Scheider et al. 1975; Kwiatkowski and Roff 1976; Yan and Stokes 1978; Yan 1979; Hendrey 1980; Hendrey et al. 1981; Yan and Dillon 1982; Eriksson et al. 1983; Findlay and Kasian 1986; Stokes 1986). Decreasing species richness with declining pH is typical, but community biomass and productivity appear unrelated to pH (Stokes 1986). Presumably, changes associated with acidification are not irreversible and might be reversed rapidly upon experimental neutralization (Bukaveckas 1989) or more slowly if and when atmospheric deposition decreases.

Mechanisms responsible for changes in the plankton community have yet to be elucidated, but may include community changes among other trophic levels (i.e. predation or changes in forage base) (Eriksson et al. 1980; Nilssen et al. 1984; Stokes 1986), altered competition, physical changes (increased transparency) (Yan 1983), chemical changes (i.e. toxicity from low pH and high metal levels (Gensemer and Kilham 1984; Stokes 1986)), or changes in nutrient concentrations (Jansson et al. 1986; Stokes 1986). Abrupt neutralization might be particularly useful in determining which responses are directly due to chemical changes. If indirect changes due to trophic interactions are important, then the response of phytoplankton communities in neutralized lakes should reflect the extent and rate at which other trophic levels change.

We examined whether phytoplankton community composition in acidic lakes in Ontario could be characterized as 'typical' of acidic systems and whether neutralization would result in reversal of these characteristics. Bowland and Trout Lakes were monitored monthly from 1982 to 1985 to document temporal

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TABLE 1. Limnological characteristics of the study lakes prior to neutralization.

	Bowland	Trout	Miskokway
Surface area (ha)	109	290	250
Mean depth (m)	7.6	12.0	14.1
Total catchment area (ha)	550	1917	3224
pH	4.9	5.8	5.6
Alkalinity ($mg \cdot L^{-1}$)	−0.32	1.03	0.75
Total Al ($\mu g \cdot L^{-1}$)	131	28	53
Secchi (m)	7.8	4.9	4.7

patterns and to determine whether any changes were attributable to neutralization (and subsequent stocking with lake trout (*Salvelinus namaycush*) in the case of Bowland Lake (Gunn et al. 1990)). Miskokway Lake was monitored as an untreated reference lake, primarily for Trout Lake because of its proximity to the latter, from 1982 to 1985. Bowland Lake was neutralized in August 1983 and Trout Lake was neutralized in May 1984 (Molot et al. 1986). Water quality changes in Bowland Lake are described in Molot et al. (1990) and zoobenthos are described in Keller et al. (1990).

Study Sites

The three study lakes are located on the Precambrian Shield in Ontario. Bowland Lake (47°05′N, 80°50′W) is located 70 km north of Sudbury. Trout Lake (45°35′N, 80°10′W) and Miskokway Lake (45°40′N, 80°14′W) are located approximately 35 km northeast of Parry Sound (165 km southeast of Bowland). Miskokway Lake is 5 km north of Trout Lake in a separate watershed. The lakes are without road access. The watersheds are forested with limited cottage development. Some relevant lake characteristics are presented in Table 1.

The lakes are oligotrophic with mean epilimnetic total P concentrations of 5 $\mu g \cdot L^{-1}$. Bowland Lake was the most acidic with an average whole-lake pH of 4.9, total Al of approximately 130 $\mu g \cdot L^{-1}$ and an alkalinity of -6 $\mu eq \cdot L^{-1}$. The pH of Trout Lake was 5.8, the total Al was 28–48 $\mu g \cdot L^{-1}$ and the alkalinity was 21 $\mu eq \cdot L^{-1}$. Immediately after treatment, the pH of Bowland increased to 6.8 and the pH of Trout increased to 6.5 (Molot et al. 1990). Miskokway Lake was a slightly coloured, acidic lake (pH 5.6, alkalinity 15 $\mu eq \cdot L^{-1}$ and total Al 48–53 $\mu g \cdot L^{-1}$). Miskokway and Trout Lakes supported diverse fish communities with reproducing lake trout populations. Bowland Lake once supported lake trout but by 1981 only one fish species remained — a reproducing population of yellow perch (*Perca flavescens*).

Methods

Sampling

Phytoplankton samples were collected monthly at 2-m depth intervals in Bowland Lake and 4-m depth intervals in Trout and Miskokway Lakes in the deep basin of each lake, from June 1982 to November 1985. One-litre volume-weighted composite samples representing the euphotic zone (assumed to be twice the Secchi depth) for taxonomic analysis, and epi-, meta-, and hypolimnetic samples for chlorophyll *a* analysis were prepared by pooling discrete samples collected with a 3-L water bottle.

Analyses

The euphotic zone samples were preserved with Lugol's iodine, concentrated 4 to 10× by sedimentation in graduated cylinders and stored in 25-mL vials for microscopic analysis. To determine biovolume, the linear dimensions of at least 300 algal entities (single cells, filaments, and colonies) were measured in each sample using an inverted microscope at 600× magnification and a Utermohl counting chamber. Biovolumes were estimated from linear dimensions by assuming simple geometric shapes.

Single epi-, meta-, and hypolimnetic composite samples from each sampling trip were stabilized with $MgCO_3$ and analyzed for chlorophyll *a* (Ontario Ministry of Environment 1983).

Statistical Analysis

Chlorophyll *a* and biovolume were tested for significant differences with the Student's *t*-test at the 1% level. We have chosen the 1% level to emphasize larger changes which are less likely to be due to annual variation. Furthermore, the posttreatment period was limited to approximately one residence time (Bowland; 3 yr, Trout; 2.5 yr, Miskokway; 1.5 yr) for the purpose of pooling data. Pooling implies that samples are obtained from the same population, hence, reacidification of a lake following treatment precludes pooling data from long time periods in order to 'smooth', or 'eliminate' short-term (year to year) variation.

Community Similarity

An instructive way of determining if phytoplankton communities have changed significantly is by an analysis of some measure of community similarity. We applied the method of Nicholls (1985) to determine if any changes observed in species composition and biovolume in Trout and Bowland Lakes after neutralization were significantly different from year-to-year differences measured in Miskokway Lake, the untreated reference lake. The expression of similarity used provides a 1:1 weighting of the community properties of both total density (cell volume) and species content (proportions). It is also a metric index that permits the use of parametric statistics for determination of significant differences. The percentage similarities were ordinated in two dimensions using a polar ordination procedure which has been shown to have advantages over other ordination techniques in floristic analyses (Allen and Skagen 1973; Whittaker and Gauch 1973; Gauch et al. 1977). Statistical levels of difference were determined more precisely from the original output of calculated percentage similarities (not from measured distances in the ordination field) by a series of unpaired *t*-tests.

The method used here (Nicholls 1985) was computerized to enable large data matrices of the type available in this study to be analyzed. For the comparisons between lakes and between treatments (pre- versus postneutralization), a total of 54 algal taxa found during the September through November periods during 1982–85 in Bowland, Trout, and Miskokway Lakes were used. Because Trout Lake was neutralized in late May of 1984 and Bowland Lake in August of 1983, the September–November time periods were selected for the phytoplankton similarity comparisons so that pre- and postneutralization comparisons among lakes could be made for identical time periods.

Results

Phytoplankton Similarities

The similarity analysis shows that autumn phytoplankton communities in Miskokway Lake (1982–85) had the highest percentage similarity of any of the lake-to-lake and year-to-year comparisons (Fig. 1). Over the 4 yr, percentage similarities of the Miskokway Lake phytoplankton communities ranged between 65.9% (for 1982 and 1985) and 75.5% (for 1982 and 1983). Trout and Bowland Lake autumn phytoplankton communities in 1982 and 1983 also had high levels of similarity between years (65.8 and 65.4%, respectively).

Neutralization of Trout and Bowland Lakes resulted in greater dissimilarities in phytoplankton composition. Surprisingly, the Trout Lake phytoplankton community became more similar to that of Miskokway Lake after neutralization although the greatest similarity should have occurred before neutralization. The most dramatic changes in Bowland Lake did not occur until the third year after neutralization; the similarity between 1982 and 1985 Bowland Lake phytoplankton was only 22.5%. This change may have been related to the dominance of *Chrysochromulina breviturrita* in 1985 and the relatively large biovolume recorded in the fall of 1985 (Fig. 2).

Similarity analysis of June and July data for 1982–87 (data not shown) also showed evidence of limited inter-annual variation. Miskokway Lake phytoplankton communities in 1982 and 1984, but not 1985 (sampling of Miskokway was discontinued after 1985), were grouped close together as were Trout Lake communities in 1982 and 1983 and Bowland Lake communities in 1982 and 1983. The Bowland Lake communities differed postneutralization but began to appear similar to the preneutralization communities by 1986. The Trout Lake communities postneutralization also differed from the preneutralization communities but remained so as of 1987. The similarity analysis of autumn and summer communities suggests that the technique is better suited to within-lake comparisons than between-lake comparisons. The findings also provide some assurance that, in the absence of whole-lake neutralization, normal year-to-year variability of phytoplankton community structure in Bowland and Trout Lakes would have been low during the study period.

Bowland Lake

Fifty-two phytoplankton taxa were recorded between June 1982 and November 1985 (Table 2). Of these, six were only recorded prior to neutralization, 15 were recorded postneutralization only and 31 were common to both periods. The majority of the 21 taxa which appeared or disappeared never exceeded 10% of the biovolume on any occasion.

To simplify analysis of the data base, a list of abundant taxa was compiled (Table 3). A taxon was considered abundant within a sample if its biovolume was greater than 10% of the total sample biovolume. Twenty-one taxa were abundant at least once during the study period. Eleven of the 21 abundant taxa were abundant at least once both before and after neutralization and seven taxa were abundant postneutralization only. Of these seven taxa which were abundant postneutralization, three were not recorded prior to neutralization (*Peridinium* sp., *P. limbatum*, and *Staurodesmus*).

The blue-green alga, *Rhabdoderma lineare*, was abundant during the summer and early fall in 1982 in acidified Bowland Lake and was abundant during the summer of 1983 until 2 d after neutralization ended. Co-abundant taxa were *Chrysosphaerella longispina* during the summer of 1982, *Botryococcus* during the summer of 1983, and *Cryptomonas*, *Dinobryon*, and *Synura* until November 1982. *Dinobryon* succeeded *Rhabdoderma* as the most common taxon in the fall of 1982 and 1983. *Rhabdoderma* was recorded postneutralization but was less than 10% of the phytoplankton biovolume on those occasions (i.e. was not classified as abundant).

The abundant, postneutralization phytoplankton taxa varied in 1984 and 1985. The chlorophytes *Botryococcus*, *Oocystis*,

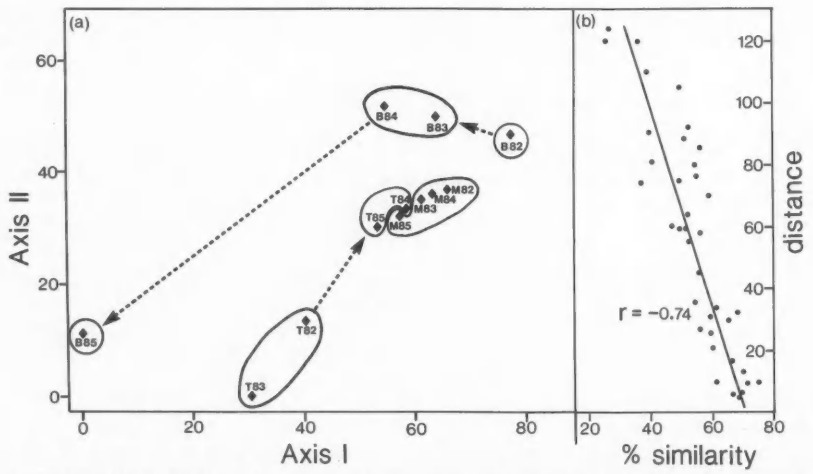

FIG. 1. Two-dimensional (polar) ordination of percentage similarities of phytoplankton assemblages in Trout Lake (T), Bowland Lake (B), and Miskokway Lake (M), for September to November 1982–85. The distance between points in the ordination field is a reasonable measure of the dissimilarity. The correlation coefficient for the linear regression of straight-line distance on percent similarity is −0.74 (Fig. 1b).

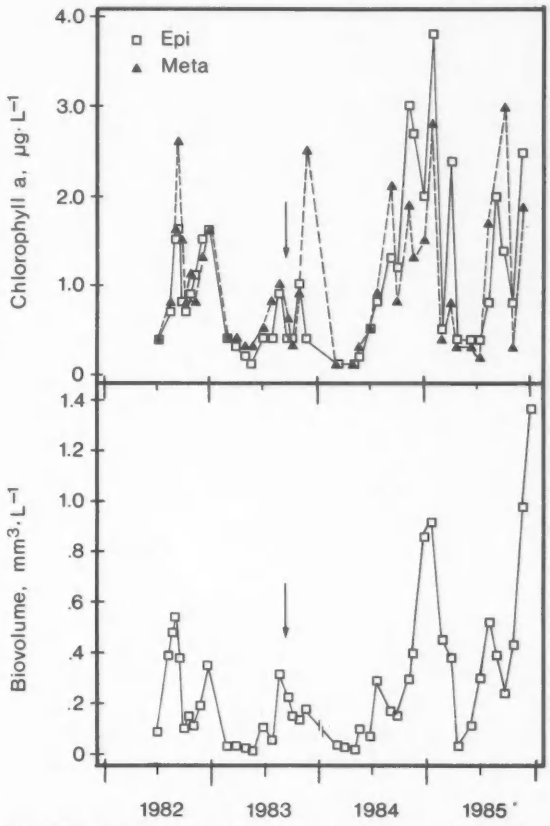

FIG. 2. Phytoplankton biovolume for the euphotic zone, and epilimnetic and metalimnetic chlorophyll *a* in Bowland Lake, 1982–85. The arrow indicates neutralization.

and *Quadrigula* were dominant only during the June peak of 1984 and the prymnesiophyte *Chrysochromulina breviturrita* was dominant during the summer of 1985. The dominant taxa during the fall peaks of 1984 and 1985 were *Synura* and *Asterionella formosa*, respectively. *Asterionella formosa* was also abundant prior to neutralization which is consistent with its classification as indifferent to pH (Dixit and Dickman 1986). Other frequently occurring abundant taxa were *Mallomonas* and an unidentified chrysophyte.

Chrysochromulina breviturrita, an odour-producing, nuisance alga associated with pH 5.5–6.2 in central Ontario lakes (Nicholls et al. 1982), first became abundant in Bowland Lake on August 1, 1984, but then remained rare (<10% of the biovolume) until February 19, 1985. A large population developed May 28–July 24, 1985. On these sample dates, the whole-lake pH ranged from 6.3–6.4 and the alkalinity ranged from 2.4–3.6 $mg \cdot L^{-1}$ (2.4–2.8 $mg \cdot L^{-1}$ while abundant in 1985).

The mean monthly ice-free phytoplankton biovolumes ($\pm$ SD) for the preneutralization period June 1982–July 1983 (0.21 ± 0.16 $mm^3 \cdot L^{-1}$, $n = 10$) and for the postneutralization period June 1984–July 1985 (0.36 ± 0.22 $mm^3 \cdot L^{-1}$, $n = 9$) were not significantly different ($p > 0.01$). There were no statistical differences between mean pre- and postneutralization chlorophyll *a* ($p > 0.01$). Mean ice-free pre- and postneutralization concentrations were 0.9 and 1.7 $\mu g \cdot L^{-1}$ in the epilimnion and 1.0 and 1.8 $\mu g \cdot L^{-1}$ in the metalimnion, respectively. Chlorophyll *a* ranged from 0.2–3.9 $\mu g \cdot L^{-1}$ during the study period.

There were two peaks, summer and fall, in phytoplankton standing crop per year (Fig. 2). The summer peak was recorded in July and August in the year of neutralization and the previous year while in the 2 yr after neutralization the summer peak occurred in late June. The fall peak in standing crop occurred after turnover each year and varied from late October to December. Annually, highest standing crops were observed after fall turnover and the postneutralization period exhibited higher peaks than in 1982. However, monthly sampling trips may not have coincided with peak standing crops (e.g. 1983). Peaks in chlorophyll *a* generally coincided with peaks in biovolume.

TABLE 2. Phytoplankton taxa present in Bowland Lake, June 3, 1982–November 21, 1985.

Bacillariophyceae:
- Achnanthes[b]
- Asterionella
- Cyclotella
- Navicula
- Nitzschia
- Synedra[b]
- Tabellaria

Chlorophyceae:
- Actinastrum[b]
- Botryococcus
- Coelastrum[b]
- Chlamydomonas
- Cosmarium[a]
- Dictyosphaerium[c]
- Elakatothrix[a]
- Gloeocystis
- Mougeotia
- Nephrocytium[c]
- Oocystis
- Pedinomonas
- Quadrigula
- Scenedesmus[a]
- Schroederia[b]
- Staurodesmus[b]
- Teilingia[b]

Chrysophyceae:
- Bitrichia
- Chrysochromulina breviturrita[b]
- Chrysochromulina parva[d]
- Chrysolykos[b]
- Chrysosphaerella longispina

Chrysophyceae (cont.):
- Dinobryon
- Epipyxis
- Kephyrion
- Mallomonas
- Salpingoeca[a]
- Spiniferomonas[b]
- Synura
- Uroglena
- Unidentified sp.

Cryptophyceae:
- Cryptomonas
- Katablepharis
- Rhodomonas

Cyanophyceae:
- Aphanothece[a]
- Chroococcus
- Lyngbya[b]
- Merismopedia[a]
- Oscillatoria[b]
- Rhabdoderma

Dinophyceae:
- Peridinium sp.
- Peridinium limbatum[c]
- Unidentified sp.

Euglenophyceae:
- Euglena[b]

Xanthophyceae:
- Isthmochloron

[a]Observed preliming only (June 1982–July 1983).
[b]Observed postliming only (September 1983–December 1984).
[c]Observed postliming only (January 1985–November 1985).
[d]*Chrysochromulina* is more correctly assigned to the Prymnesiophyceae, but has been included in the Chrysophyceae for convenience. The identification of *C. breviturrita* may include some *C. laurentiana* which can be distinguished only on the basis of electron microscopic structure of their organic scales.

Trout and Miskokway Lakes

Sixty-nine phytoplankton taxa were observed in Trout Lake and 71 were observed in Miskokway Lake between July 1982 and November 1985 (Tables 4 and 5). Fifty-seven taxa were common to both lakes. None of the 26 taxa unique to either lake exceeded 10% of the biovolume at any time during the study period.

TABLE 3. Occurrence of abundant (>10% of the biovolume) phytoplankton taxa in Bowland Lake before liming (June 3, 1982–July 19, 1983) and after liming (August 18, 1983–November 21, 1985). The number in brackets refers to the frequency of occurrence in which the taxon was >10%. The total number of samples was 43.

Abundant prior to liming only		Abundant both before and after liming		Abundant after liming only	
Chroococcus	(1)	Asterionella[b]	(5)	Chlamydomonas	(1)
Chrysosphaerella longispina	(5)	Botryococcus	(7)	Chrysochromulina breviturrita	(5)
Rhabdoderma[a]	(10)	Cryptomonas	(15)	Cyclotella	(3)
		Dinobryon	(13)	Peridinium sp.[c]	(2)
		Gloeocystis	(3)	Quadrigula	(1)
		Mallomonas	(18)	Peridinium limbatum[d]	(1)
		Oocystis	(3)	Staurodesmus[d]	(2)
		Synura	(12)		
		Uroglena	(3)		
		Unidentified chrysomonads	(15)		
		Unidentified dinoflagellates	(3)		

[a]Abundance ended less than 2 wk after liming.
[b]Abundant prior to liming and 2 yr after liming.
[c]Abundant immediately after liming only.
[d]Abundant 1985 only.

The abundant (>10% of the biovolume) taxa were similar in both lakes (Tables 6 and 7). The major difference was that the chrysophyte *Synura* was frequently abundant in Miskokway Lake during fall and winter periods, but was abundant only in the winter of 1983–84 in Trout Lake prior to neutralization. Diatoms, primarily *Rhizosolenia* and *Tabellaria flocculosa* (the latter is classified as acidophilous with widest distribution in slightly acidic lakes (Dixit and Dickman 1986), and chrysophytes dominated both lakes throughout the study period. The chrysophytes *Synura* and *Chrysosphaerella longispina* were abundant in Trout Lake only prior to neutralization. Three chrysophyte taxa, including *C. longispina*, were abundant before June 5, 1984 in Miskokway Lake but were not abundant after that date. Hence, the composition of abundant taxa was similar in both lakes during the study period, with the exception of *Synura*.

Asterionella formosa was the dominant *Asterionella* species and *Tabellaria flocculosa* was the dominant *Tabellaria* species both before and after neutralization in Trout Lake.

Chrysochromulina breviturrita was recorded in 53% of the samples taken from Trout, Miskokway, and postneutralization Bowland Lakes, but was recorded only once in 17 samples taken from Bowland Lake prior to neutralization (Table 8). This suggests that conditions in Bowland Lake prior to neutralization were probably outside the physiological range of conditions necessary for growth, whereas the growing conditions during the peak growth period in 1985 in Bowland Lake were within the range as reported by Wehr et al. (1985). Although neutralization apparently promoted increased abundance of *C. breviturrita* in Bowland Lake, nuisance odours were never noted, unlike other lakes.

The mean (± SD) ice-free biovolumes in Trout Lake, excluding June 5 and 6, 1984 because of the transitional nature of the period, were 0.52 ± 0.24 mm$^3 \cdot$L^{-1} ($n = 11$) preneutralization and 0.47 ± 0.36 mm$^3 \cdot$L^{-1} ($n = 14$) postneutralization. Ice-free pre- and postneutralization chlorophyll *a* concentrations (mean ± SD) were 1.6 ± 1.0 and 1.4 ± 0.5 μg$\cdot$L^{-1} (epilimnion), respectively, and 2.0 ± 1.3 and 2.5 ± 1.8 μg$\cdot$L^{-1} (metalimnion), respectively. The chlorophyll and biovolume changes were not significant at the 1% level.

The mean (± SD) ice-free phytoplankton biovolumes in Miskokway Lake were 0.37 ± 0.28 mm$^3 \cdot$L^{-1} ($n = 11$) for September, 1982–May 1984 and 0.36 ± 0.22 mm$^3 \cdot$L^{-1} ($n = 14$) for June 1984–November 1985. Ice-free pre- and postneutralization chlorophyll *a* concentrations (mean ± SD) were 1.4 ± 0.5 and 2.1 ± 1.3 μg$\cdot$L − 1 (epilimnion), respectively, and 2.4 ± 2.6 and 2.1 ± 1.3 μg$\cdot$L^{-1} (metalimnion), respectively. There were no statistically significant changes ($P > 0.01$) in biovolume or chlorophyll *a* in Miskokway Lake or between Trout and Miskokway Lakes either prior to or after neutralization.

Temporal distributions tended to be bimodal (Fig. 3 and 4). Relatively brief fall peaks may not have been recorded because of the monthly sampling frequency.

Discussion

Our experimental design does not readily permit separation of annual fluctuations from treatment effects except where responses are large or unusual in relation to annual fluctuations. However, the results of the percentage similarity analysis provide some assurance that, in the absence of whole-lake neutralization, normal year-to-year variability of autumn phytoplankton community structure would have been low in Bowland and Trout Lakes during the study period.

Mean ice-free (May–November) biovolumes and chlorophyll *a* levels did not differ significantly at the 1% level between pre- and postneutralization periods, or between Trout and Miskokway Lakes. The observed changes were likely within the limits of annual variation. However, mean biovolume in Bowland Lake increased by 75% whereas biovolumes decreased by less than 10% in Trout and Miskokway Lakes. Long-term changes in community size did not occur in several neutralized lakes in Norway (Brettum and Hindar 1985) and in Ontario (Yan and Dillon 1982).

Yan (1979) demonstrated that phytoplankton biomass was better correlated with total phosphorus (TP) concentrations than pH in Sudbury area lakes. Hence, the lack of change in phy-

TABLE 4. Phytoplankton taxa present in Trout Lake, July 1982–November 1985.

Bacillariophyceae:	Achnanthes[b,c]	Navicula[a]
	Asterionella	Nitzschia[c]
	Cyclotella	Rhizosolenia
	Diatoma[b,c]	Synedra
	Fragilaria[b,c]	Tabellaria
	Melosira	
Chlorophyceae:	Arthrodesmus	Mougeotia[c]
	Botryococcus	Nephrocytium
	Carteria[a,c]	Oocystis
	Chlamydomonas	Pediastrum[c]
	Coelastrum	Pedinomonas[a]
	Cosmarium	Planktonema
	Crucigenia	Quadrigula
	Dictyosphaerium	Scenedesmus
	Elakatothrix[a]	Sphaerozosoma
	Euastrum[b,c]	Spondylosium[a]
	Gloeocystis	Staurastrum
	Koliella	Teilingia[a,c]
	Monoraphidium	Tetraedron
Chrysophyceae:	Bitrichia	Kephyrion
	Chrysochromulina breviturrita[d]	Mallomonas
	Chrysochromulina parva[d]	Salpingoeca
	Chrysolykos	Spiniferomonas
	Chrysosphaerella coronacirc.	Synura
	Chrysosphaerella longispina	Uroglena
	Dinobryon	Unidentified sp.
Cryptophyceae:	Cryptomonas	Katablepharis
	Rhodomonas	
Cyanophyceae:	Anabaena	Lyngbya[a]
	Apanothece	Merismopedia
	Aphanocapsa[b]	Microcystis
	Chroococcus	Rhabdoderma
	Coelosphaerium	
Dinophyceae:	Unidentified sp.	
Euglenophyceae:	Unidentified sp.[a,c]	
Xanthophyceae:	Centritractus[a,c]	Ophiocytium[a]
	Isthmochloron[c]	

[a]Observed preliming only.
[b]Observed postliming only.
[c]Not observed in Miskokway Lake.
[d]*Chrysochromulina* is more correctly assigned to the Prymnesiophyceae, but has been included in the Chrysophyceae for convenience. The identification of C. *breviturrita* may include some C. *laurentiana* which can be distinguished only on the basis of electron microscopic structure of their organic scales.

TABLE 5. Phytoplankton taxa present in Miskokway Lake, July 1982–November 1985.

Bacillariophyceae:	Asterionella	Navicula[a]
	Cyclotella	Rhizosolenia
	Eunotia[b]	Synedra
	Melosira	Tabellaria
Chlorophyceae:	Actinastrum[b]	Nephrocytium[a]
	Ankistrodesmus[b]	Oocystis
	Arthrodesmus	Pedinomonas
	Botryococcus	Planktonema
	Chlamydomonas	Quadrigula
	Closterium[b]	Scenedesmus
	Coelastrum	Selenastrum[a,b]
	Cosmarium	Sphaerocystis[a,b]
	Crucigenia	Sphaerozosoma
	Dictyosphaerium	Spondylosium[a]
	Elakatothrix[a]	Staurastrum
	Gloeocystis	Staurodesmus
	Kirchneriella[b]	Tetraedron
	Koliella[a]	Unidentified coccoid[a,b]
	Monoraphidium	
Chrysophyceae:	Biocoeca[b]	Kephyrion
	Bitrichia	Mallomonas
	Chrysochromulina breviturrita[c]	Salpingoeca
	Chrysochromulina parva[c]	Spiniferomonas
	Chrysolykos	Stelexomonas[b]
	Chrysosphaerella coronacirc.	Synura
	Chrysosphaerella longispina	Uroglena
	Dinobryon	Unidentified sp.
	Epipyxis[a,b]	
Cryptophyceae:	Cryptomonas	Katablepharis
	Rhodomonas	
Cyanophyceae:	Anabaena	Eucapsis[a,b]
	Aphanizomenon[b]	Lyngbya[a]
	Aphanocapsa	Merismopedia
	Aphanothece[a]	Microcystis
	Chroococcus	Oscillatoria[b]
	Coelosphaerium	Rhabdoderma
Dinophyceae:	Unidentified sp.	
Xanthophyceae:	Ophiocytium[a]	

[a]Observed after June 20, 1984 only.
[b]Not observed in Trout Lake.
[c]*Chrysochromulina* is more correctly assigned to the Prymnesiophyceae, but has been included in the Chrysophyceae for convenience. The identification of C. *breviturrita* may include some C. *laurentiana* which can be distinguished only on the basis of electron microscopic structure of their organic scales.

toplankton biovolume and chlorophyll *a* after neutralization is not unexpected because the application of calcite did not result in measurable changes in TP in Bowland Lake (Molot et al. 1990) or Trout Lake (L. A. Molot, unpubl. data).

The phytoplankton community in Bowland Lake, despite the low pH (4.9) prior to neutralization, did not resemble communities in nearby acidified Sudbury lakes or in Scandinavian lakes which were dominated by dinoflagellates (Hultberg and Anderson 1981; Eriksson et al. 1983; Yan and Lafrance 1984; Yan and Miller 1984). Although Trout and Miskokway Lakes were not as acidic as Bowland, several of the abundant taxa were common to all three lakes — *Asterionella, Cryptomonas* and *Mallomonas* (Tables 3, 6 and 7).

The ecological significance of the appearance and disappearance of taxa as a function of treatment in these study lakes is difficult to evaluate. These taxa were primarily rare (never abundant) and rare taxa are more susceptible to 'sampling and counting error' than are abundant taxa. A more frequent sampling schedule may have recorded them.

Changes in individual taxa were the most apparent responses of the lakes to treatment. Of the four taxa which were abundant only before neutralization in Trout and Bowland Lakes, three can be said to have been affected by the treatment (*Synura, Rhabdoderma*, and *Chroococcus*) on the grounds that they were not abundant after neutralization in any of the lakes. *Chrysosphaerella longispina* was not abundant after neutralization in Trout and Bowland Lakes, but it was also not abundant in the reference lake after 1984. Therefore, control of *C. longispina* by other factors common to all three lakes cannot be ruled out.

The absence of any taxa in Trout Lake which were abundant only after neutralization (Table 6) suggests that changes brought about by treatment were too small to exploit. The appearance of six taxa in Bowland Lake which were abundant only in the postneutralization period suggests that changes were large

TABLE 6. Occurrence of abundant (>10% of the biovolume) phytoplankton taxa in Trout Lake before liming (September 1982–May 1984) and after liming (June 1984–November 1985). The numbers in brackets refer to the frequency of occurrence in which the taxon was >10%. The total number of samples was 36.

Abundant prior to liming only[a]		Abundant both before and after liming		Abundant after liming only
Chrysosphaerella longispina	(3)	Asterionella	(7)	—
Synura	(2)	Cryptomonas	(8)	
		Cyclotella	(8)	
		Mallomonas	(5)	
		Rhizosolenia	(16)	
		Synedra	(5)	
		Tabellaria	(20)	
		Unidentified dinoflagellates	(7)	
		Unidentified chrysomonads	(6)	

[a]Observed postliming but less than 10% of biovolume.

TABLE 7. Occurrence of abundant (>10% of the biovolume) phytoplankton taxa in Miskokway Lake before and after June 5, 1984. The number in brackets refer to the frequency of occurrence in which the taxon was >10%. The total number of samples was 35.

Abundant September 1982–May 1984 only[a]		Abundant both periods		Abundant June 1984–November 1985 only	
Chrysochromulina breviturrita	(1)	Asterionella	(4)	Uroglena[b]	(1)
Chrysosphaerella longispina	(2)	Cryptomonas	(10)		
Dinobryon	(3)	Cyclotella	(4)		
		Mallomonas	(2)		
		Rhizosolenia	(17)		
		Synura	(18)		
		Tabellaria	(12)		
		Unidentified dinoflagellates	(3)		
		Unidentified chrysomonads	(9)		

[a]These taxa were observed during both periods but were abundant only before June 5, 1984.
[b]Uroglena was also observed prior to June 5, 1984.

TABLE 8. Frequency of occurrence of *Chrysochromulina breviturrita*.

	Bowland	Trout	Miskokway[a]
Preliming:			
Number of occurrences recorded	1	12	11
Number of samples taken	17	17	19
Number of times >10% of biovolume	0	0	1
Postliming:			
Number of occurrences recorded	15	6	6
Number of samples taken	25	17	17
Number of times >10% of biovolume	5	0	0

[a]Miskokway Lake was a reference lake for Trout Lake and was not neutralized.

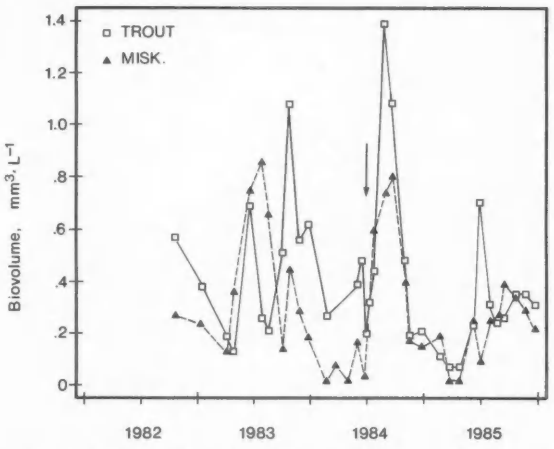

FIG. 3. Phytoplankton biovolume for the euphotic zone in Trout and Miskokway Lakes, 1982–85. The arrow indicates neutralization of Trout Lake.

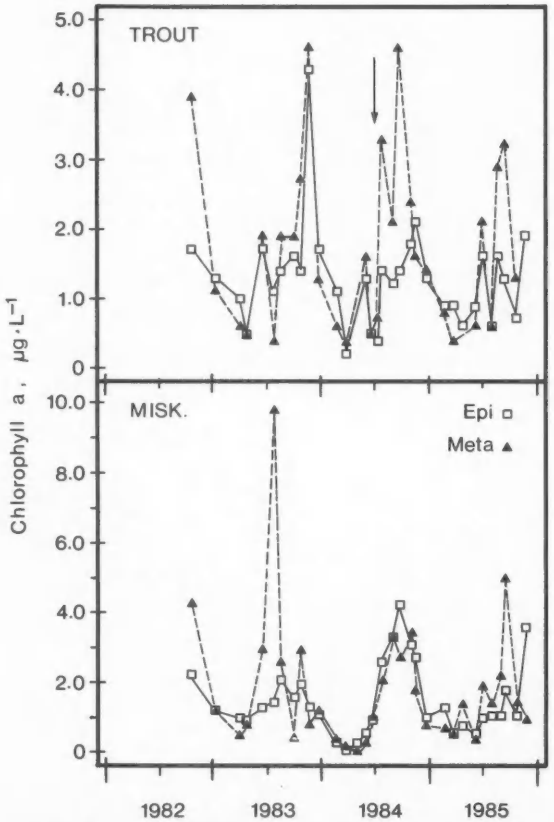

FIG. 4. Epilimnetic and metalimnetic chlorophyll *a* in Trout and Miskokway Lakes, 1982–85. The arrow indicates neutralization of Trout Lake.

enough to exploit, particularly for *Chrysochromulina breviturrita* which was abundant five times (Table 3).

The distribution of *C. breviturrita* in our study lakes (Table 8) is consistent with other findings. *C. breviturrita* populations, which are sometimes associated with odours, have developed in central Ontario lakes with pH 5.5–6.2 (Nicholls et al. 1982). A pH tolerance range of 4.0–6.9, an upper alkalinity limit of 5 $mg \cdot L^{-1}$ and an absolute Se requirement has been established for an isolate of *C. breviturrita* from central Ontario (Wehr and Brown 1985; Wehr et al. 1985). This species can be expected to occur as neutralized lakes reacidify.

King (1970) proposed that nuisance blue-green algae dominated eutrophic waters because of their ability to utilize extremely low concentrations of free CO_2, whereas eucaryotic algae were less efficient, although high levels of HCO_3^- (>100 μM) typically occur in eutrophic waters. An analogous situation may develop in acidified lakes such as Bowland in which both very low free CO_2 and HCO_3^- levels occur (Molot et al. 1990). At pH <5, HCO_3^- is virtually absent. Epilimnetic CO_2 concentrations were frequently below the detection limit of 17 μM during the summer of 1983 in Bowland Lake, but were 28–41 μM during the summer following neutralization. This may explain the abundance of *Rhabdoderma* in Bowland Lake prior to neutralization (and the abundance of *Anabaena* in July 1988). The prevalence of blue-green algae has been observed in other acidic lakes in the Killarney area in Ontario (Kwiatkowski and Roff 1976), Beaverskin Lake in Nova Scotia (Blouin et al. 1984), and experimentally acidified Lake 223 in northwestern Ontario in 1980 and 1981 when the pH was held at 5.0 (Findlay and Kasian 1986). Low free CO_2 levels may occur in acidified lakes because of decreased decomposition rates of freshly sedimented detritus (Kelly et al. 1984), or because of increased demand for free CO_2 in the absence of HCO_3^-. Changes in alkalinity affect HCO_3^- concentration but do not affect free CO_2 in solutions at atmospheric equilbrium; however, relative proportions of inorganic C species change with changing alkalinity (Stumm and Morgan 1981).

Hornstrom et al. (1984) suggested that phytoplankton community structure is affected by a combination of acidity, metals, and nutrient depletion. This might explain why dinoflagellates were dominant in several metal-contaminated Sudbury area lakes with pH <5.0 (Yan and Miller 1984) and in acidified Scandinavian lakes (Hultberg and Anderson 1981; Eriksson et al. 1983), but were not dominant in the Killarney area or in Bowland Lake at similar pH (Kwiatkowski and Roff 1976).

The trend to increasing phytoplankton biomass in Bowland Lake after neutralization may be related to decreasing crustacean zooplankton biomass although other factors cannot be ruled out. The mean ± SD crustacean biomass decreased from 44.4 ± 19.9 μg dry $wt \cdot L^{-1}$ preneutralization to 24.2 ± 21.0 postneutralization (not significant at the 1% level). The crustacean community was dominated by *Diaptomus minutus* during the entire study period. Interestingly, ciliate and rotifer biomasses also increased after neutralization from a total of 1.43 to 5.03 μg dry $wt \cdot L^{-1}$ although the differences were not significant at the 1% level. The major change in the rotifer community was the decrease in *Keratella taurocephala* after neutralization.

Mean whole-lake crustacean zooplankton biomass in Trout Lake also decreased from 30.7 ± 25.3 μg dry $wt \cdot L^{-1}$ before neutralization to 23.1 ± 14.1 after neutralization. Rotifer and ciliate biomasses increased (2.17 to 2.49 μg dry $wt \cdot L^{-1}$ total). Mean whole-lake crustacean zooplankton biomass in Miskokway Lake decreased from 17.1 ± 11.1 μg dry $wt \cdot L^{-1}$ before neutralization of Trout Lake to 13.5 ± 7.6 after neutralization. Rotifer biomass decreased and ciliate biomass increased (total dry weight increased from 3.29 to 3.74 $\mu g \cdot L^{-1}$). Hence, crustacean biomass decreased in both treated lakes as well as the reference lake during the study period.

Blue-green algal abundance decreased after neutralization in Bowland Lake concomitant with decreased crustacean biomass. Since blue-green algae are considered relatively unsuitable as food (Burns 1968*a*, 1968*b*; Infante and Abella 1985) and, therefore, eucaryotic algae receive disproportionately more grazing pressure, it is conceivable that reduced grazing pressure after neutralization expedited replacement of *Rhabdoderma*. However, zooplankton grazing pressure alone is an unlikely explanation for the abundance of *Rhabdoderma* prior to neutralization since blue-green algae would then be far more common in circum-neutral oligotrophic systems with high grazing pressure. We postulate that chemical conditions prior to neutralization must be more favourable for growth of *Rhabdoderma*.

In contrast to the insignificant changes in phytoplankton standing crops reported here, large changes were observed in experimentally acidified Lake 223 in biomass between pretreatment years (1975–76 with pH 6.6–6.7) and later years (1981–83 with pH 5.0–5.1) (Findlay and Kasian 1986). Perhaps these changes were related to relatively large changes in trophic interactions (Schindler et al. 1985) such as decimation of the fish community. While acidification can cause major food chain disruptions as fish populations disappear, neutralization will not cause major short-term disruptions unless extinct fish populations are restored to previous levels (e.g. see Keller et al. 1990). In the case of Trout Lake, fish populations did not appear to be affected by acidification or neutralization (J. M. Gunn, unpubl. data).

Large phytoplankton changes also occurred immediately after application of very large amounts of calcite to acidified Cranberry Pond and Woods Lake in the Adirondack Mountains (Bukaveckas 1989). Large reductions in chlorophyll and cell densities occurred, probably because of flocculation. The resulting large changes in water chemistry and depleted populations may have created opportunities for new species to exploit.

Keller et al. (1990) concluded that the large 1983 cohort of yellow perch (*Perca flavescens*) (Gunn et al. 1990) in Bowland Lake was probably responsible for many of the changes in the zoobenthos community in subsequent years. The perch cohort may also have caused the smaller postneutralization crustacean zooplankton biomass and, therefore, the higher phytoplankton standing crop although in spite of major changes in the fish community in Bowland Lake, changes in the annual ice-free phytoplankton standing crop were not significant at the 1% level (or 10%). However, crustacean decreases were also recorded in Trout and Miskokway Lakes, although changes in the fish communities were not noted. It is likely that the major phytoplankton taxonomic changes (the responses of *Rhabdoderma* and *Chrysochromulina breviturrita*) were responses to chemical changes.

Although neutralization altered the physico-chemistry of Bowland and Trout Lakes, it is not possible to determine precisely which taxa were directly affected by chemical changes without laboratory culturing and were points of entry for a "cascading" effect through the food web and which taxa responded to biological changes. The physico-chemical con-

ditions extant in a system create a subset of species at each trophic level capable of growing and reproducing. Regardless of trophic interactions such as grazing pressure, competition, food availability, etc., the system must be tolerated physiologically by those present. Hence, physico-chemical conditions are always a primary constraint on community composition. Within the subset of all possible species, trophic interactions, along with other factors such as colonization rates, result in the observed communities.

The average standing crops of the phytoplankton, zooplankton, and zoobenthos communities were relatively unaffected by treatment although taxonomic changes occurred, even in Bowland Lake, the lake in which the greatest chemical change occurred and in which the fish community was altered the most (Gunn et al. 1990; Keller et al. 1990; Molot et al. 1990). This suggests that taxonomic changes maintained stability of the lakes (with respect to standing crops and by inference, energy flow) under chemical stress.

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Effects of Neutralization and Early Reacidification on Filamentous Algae and Macrophytes in Bowland Lake

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Within one year of neutralizing Bowland Lake (pH 4.8–5.5 increased to 6.3–6.7), previously extensive growths of filamentous algae et (*Mougeotia* and *Zygogonium*, >10 and 100% shoreline coverage, respectively) were essentially eliminated (<1% shoreline coverage). Reacidification in the second year (pH 5.7–6.7) was accompanied by increased submerged epilithic and epiphytic growths of predominantly *Zygogonium*, often to preliming coverage. As found in other studies, pH ≥6.0 appears to represent a threshold relative to the predominance of certain filamentous algae in softwater lakes. The short time between the change in acidity and the disappearance and reappearance of the filamentous algae suggests that they may be important biological indicators or predictors of acidification and its reversal. The changes in pH and alkalinity following neutralization did not substantially affect the macrophyte community in Bowland Lake. Macrophytes were restricted primarily to littoral areas less than 3 m in depth, despite excellent water transparency both before (SD = 8.0 m, 1982) and after neutralization (SD = 4.5 m, 1985). Two uncommon species observed prior to neutralization (*Eleocharis parvula* and *E. acicularis*) were not observed afterwards, while two new and uncommon species (*Nitella* sp. and *Brasenea schreberi*) were.

Un an après la neutralisation du lac Bowland (passage du pH de 4.8–5.5 à 6.3–6.7), les proliférations d'algues filamenteuses (*Mougeotia* et *Zygogonium*, respectivement >10 et 100 % de couverture à la ligne de rivage) avaient pratiquement disparu (<1 % de couverture à la ligne de rivage). La réacidification de la deuxième année (pH 5,7–6,7) s'est accompagnée de poussées d'épilithon et d'épiphyton submergés, constitués surtout de *Zygogonium*, la couverture retrouvant souvent le niveau antérieur au chaulage. Comme l'ont montré d'autres études, un pH de ≥6.0 semble représenter un seuil marquant la prédominance de certaines algues filamenteuses dans les lacs dont l'eau est douce. La brièveté de l'intervalle entre la modification de l'acidité et la disparition ou la réapparition des algues filamenteuses semble indiquer que ces espèces peuvent être des indicateurs ou des prédicteurs biologiques importants de l'acidification ou de son renversement. Les modifications du pH et de l'alcalinité suite à la neutralisation n'ont pas affecté de façon importante la communauté macrophytique du lac Bowland. les macrophytes étaient confinés avant tout aux zones littorales de moins de 3 m de profondeur, malgré la très grande transparence de l'eau tant avant (ECT = 8.0 m au disque de Secchi, 1982) qu'après la neutralisation (ECT = 4.5 m, 1985). Deux espèces peu communes observées avant la neutralisation (*Eleocharis parvula* et *E. acicularis*) n'ont pas été observées par la suite, tandis que deux espèces nouvelles et peu communes (*Nitella* sp. et *Brasenea schreberi*) l'ont été.

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Since the early 1970's, with the recognition of acid precipitation as a major environmental problem, increasing attention has been paid to the effect of acidification of freshwater habitats on the growth of periphyton, especially filamentous algae (Hendrey 1976; Muller 1980; Stokes 1981). Increased accumulations of filamentous algae, almost invariably Zygnematales, appear to be one of the earliest and most conspicuous signs of acidification (Turner et al. 1987). Excessive algal biomass can have a number of unwanted effects including: fouled swimming areas, reduced appeal of shoreline areas and possible impacts on fish and other aquatic life (MOE 1987). Our knowledge of the ecology and taxonomy of softwater filamentous algae remains inadequate. Nevertheless, recent studies have generated new insights into mechanisms affecting the growth of filamentous algae in acidified and acidifying systems (see review by Stokes 1986).

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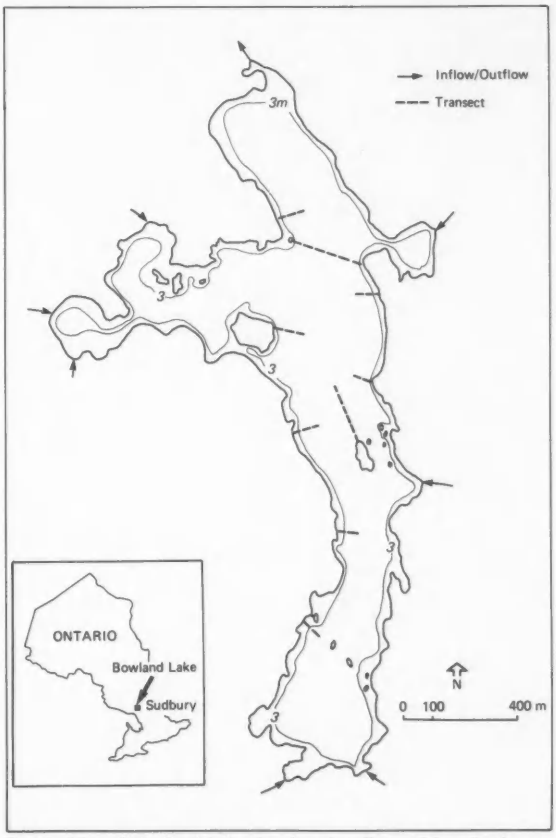

FIG. 1. Map of Bowland Lake showing shoreline and 3-m depth contour. Macrophyte transects (seven shallow water and two deep water) were surveyed in 1982.

In Scandinavia and North America, experimental neutralization of lakes and watersheds has been used to mitigate the effects of elevated acidity and reestablish sports fisheries (Hasselrot and Hultberg 1984; Rosseland and Skogheim 1984; Scheider and Brydges 1984). The impact of lake neutralization on filamentous algal communities has not been evaluated quantitatively, but evidence to date indicates that neutralization reduces the amount of filamentous algae present (Lazarek 1981; Hultberg and Andersson 1982).

The littoral macrophyte community is an important component of lake ecosystems because of its impact on nutrient cycling, the contribution of organic matter and the unique habitat offered for epiphytic algae, zooplankton, and fish (Wetzel 1981). Descriptive surveys of macrophyte communities over a range of chemical conditions have shown that species richness decreases with pH (Roberts et al. 1985; Wile et al. 1985; Catling et al. 1986), while Yan et al. (1985) found no change in tracheophyte (macrophytes minus charophytes and bryophytes) species richness with pH, as long as trace metals were low. Yan et al. (1985), however, found a negative relationship between bryophyte richness and pH, and also showed that charophytes were absent in lakes with pH <5.2. Hence potential changes in macrophyte and associated communities could occur in acidified lakes after neutralization.

TABLE 1. Selected epilimnetic (ice-free) and 0–6 m (ice-covered) water chemistry, Bowland Lake 1982–85. Liming occurred in August 1983. Data are mean values followed by ± SD, the number of observations in parenthesis, and the range. ND = no data.

	Year	pH	DIC ($mg \cdot L^{-1}$)	Secchi (m)	Chlorophyll *a* ($\mu g \cdot L^{-1}$)
Preliming	1982	5.2 ±0.1(9) 5.11–5.46	ND	7.6 ±0.8(10) 6.0–8.0	1.1 ±0.4(10) 0.4–1.6
	1983	5.0 ±0.2(7) 4.78–5.23	0.3 ±0.1(7) 0.2–0.4	6.2 ±1.5(7) 4.0–8.0	0.4 ±0.2(7) 0.1–0.9
Postliming	1983	6.9 ±0.2(4) 6.6–7.0	1.2 ±0.1(4) 1.0–1.3	7.3 ±1.4(4) 5.2–8.0	0.1 ±0.0(4) 0.0–0.1
	1984	6.6 ±0.2(12) 6.3–6.7	1.3 ±0.4(11) 0.8–1.9	5.3 ±0.9(12) 3.0–6.5	1.3 ±1.3(12) 0.7–3.8
	1985	6.5 ±0.3(10) 5.7–6.7	1.0 ±0.3(10) 0.6–1.4	4.6 ±0.8(10) 3.0–6.0	1.2 ±0.8(10) 0.4–2.5

In this study we document some effects of neutralization and early reacidification on filamentous algae and macrophyte communities in Bowland Lake, Ontario, and interpret the observed changes in light of suspected growth-controlling factors. This work was conducted as a contribution to the Experimental Lake Neutralization Programme of the Ontario Ministries of the Environment and Natural Resources.

Background

Bowland Lake (Fig. 1) is located on the Precambrian Shield, approximately 70 km north of Sudbury, Ontario (47°05′N 80°50′W). The lake surface area, of which the littoral zone (to 3 m depth) comprises about 22% is 109.4 ha. Maximum and mean depths are 28 and 7.6 m, respectively, and the watershed area is 441 ha.

The water quality of Bowland Lake before and after neutralization is discussed in Molot et al. (1990). In summary, prior to neutralization, Bowland Lake was clear (Secchi depth 4.0–8.0 m), oligotrophic (chlorophyll *a* 0.10–1.60 $\mu g \cdot L^{-1}$) and acidified (dissolved inorganic carbon (DIC) 0.2–0.4 $mg \cdot L^{-1}$; pH 4.8–5.5). Following neutralization in August 1983, changes occurred in epilimnetic water quality that were potentially important to the growth of filamentous algae and macrophytes: Secchi depth decreased, while pH and DIC increased (Table 1). Reacidification of Bowland Lake is expected to be rapid, with pH and alkalinity returning to premanipulation levels within 9 yr (Molot et al. 1990).

Methods

Filamentous Algae

In the littoral zone of Bowland Lake, all major visible growths of filamentous algae attached to rocks, logs, and macrophytes, or occurring as unattached aggregations, were mapped annually from 1982 to 1985. This study is the first, aside from Turner et al. (1987), to quantitatively assess the shoreline development of filamentous algae in an acid-stressed lake.

Field activities were carried out from the surface by two individuals working from a small motor boat. Depending upon weather conditions and algal complexity and abundance, two to four days were required to complete each annual lake survey (except in 1985 as indicated below). When possible, surveys were carried out to coincide with peak littoral algal biomass (typically mid August to early September as observed by M. B. Jackson, unpubl. data). In 1983, the survey was carried out in early August immediately prior to neutralization. In 1985 only a qualitative assessment was made: the entire lake shoreline was surveyed rapidly (several hours duration) and algal growth characteristics were estimated from an overall impression rather than from the more detailed procedure described below. The 1985 collection and analysis of taxonomic samples, however, remained unchanged from other years.

To effectively view algae through lake surface glare, a wide-brimmed hat and polaroid sunglasses were helpful. A clear acrylic-bottomed bucket was also useful for viewing under windy or poor light conditions. We found that a portable golfball retriever, extendable to approximately 4 m in length, and with a folding rake, was our most useful tool for collecting algae deeper than 2 m. For shallower collections, and for general use, a small kitchen strainer (10 cm in diameter) attached to a wooden broom handle (1.5–2 m in length) was useful.

Before commencing each annual mapping effort, a preliminary survey was made of selected stretches of shoreline to establish (or reaffirm) the relationships between taxonomy and visible/tactile algal characteristics. Visible/tactile algal characteristics included appearance, texture, physical dimensions, depth distribution, substratum associations, etc. A Swift FM-31 portable microscope was used to verify the taxonomic consistency of the different algal species/communities based on different visible/tactile algal characteristics observed in the field.

Once algal communities with consistent taxonomic make-up were established, mapping was initiated. On a shoreline map of the lake (scale = 1:4000), each occurrence of every community pattern was labelled sequentially (1 to *n*), and the length of shoreline covered was depicted to scale. Lengths of shoreline covering less than 50–100 m were usually estimated in the field, while longer lengths were measured later with a Dietzgen plan measure model 1723. Upper and lower depths (the estimated average depths at which algal biomass was noticeably greater than at lesser or greater depths, respectively) and growth thickness within the area bounded by upper and lower depths and length of shoreline covered (the estimated average thickness) were recorded. Note that we defined the area between our upper and lower depths as the zone in which most, but not necessarily all, of the algal biomass occurred. Growth often extended to shallower and deeper depths in less abundance. In our investigations in Bowland Lake and Lake 302 South (Turner et al. 1987), the maximum depth for a community pattern depicted (as in Table 2) represents a lake-weighted mean value for significant growth. This mean value is influenced by local substratum availability, especially for epiphytic algae, and possibly water movement, and should not be misinterpreted as representing the maximum depth to which growths actually occur (Stokes 1986).

For each pattern, lake-weighted expressions of upper and lower depth and growth thickness were determined by multiplying values for individual occurrences by the corresponding length, summing the results, and dividing by the lake perimeter. An expression of algal development (the percent of total shoreline length covered) was obtained by summing all individual lengths of occurrence, dividing by the lake perimeter, and multiplying by 100.

Algal samples were selected from growths representative of each pattern. A minimum of three samples of each community pattern was collected for later detailed taxonomic analysis. About 5 mL of each drained algal sample was placed in a 25-mL vial. The vial was filled with lake water and 0.5 mL of acid Lugol's solution added to preserve the sample (0.1 mL of formalin was added later for long-term preservation). In the laboratory, subsamples were analyzed with a light microscope at 400× magnification to identify algal filaments to genus. The samples were identified based on standard taxonomic references (Nurulislam 1963; Gauthier-Lièvre 1965; Starmach 1966; Mrozinska-Webb 1969; Bourelly 1970; Bourelly 1972; Kadlubowska 1972; Starmach 1972; Prescott 1982; Kadlubowska 1984). The percent contribution of each genus was estimated in terms of biovolume (at 150×) by averaging the results of duplicate analyses on all three vials.

Colour photography was used to record the field appearance of samples for later reference. To photograph algae through the lake surface, we used an automatic Al Canon equipped with a polaroid filter (to eliminate surface glare) and Kodachrome 64 ASA slide film. We overexposed each photograph by one f-stop to ensure good exposure of the invariably darker than background subject matter.

Macrophytes

Approximately 60% of the Bowland Lake littoral zone was surveyed in 1982 and 1985 for macrophytes. To determine the depth distribution of macrophytes in Bowland Lake, seven shallow water transects (0–10 m) and two deep water transects (0–26 m max.) were surveyed by SCUBA divers in 1982. Previous reports of Secchi disc readings (Molot et al. 1990) suggested that macrophytes might grow to a maximum depth of 18 m. Macrophytes were not observed deeper than 3 m and were observed mainly at depths less than 2 m. The littoral zone, surveyed to 3 m depth, was divided into 114 sections based on substratum types (rocks, sand/gravel, detritus, logs/branches). Sections consisting of only rock and sections biased by human influence were not resurveyed in 1985. Statistical differences in percent shoreline coverage were tested using *t*-tests.

The macrophyte species within each section were identified according to Muenscher (1944); Fassett (1960); Hotchkiss (1967) and compared to dry mount samples from the Botany Department, University of Toronto.

Results

Filamentous Algae

During both preneutralization years, 1982 and 1983, the shallow littoral zone of Bowland Lake was largely covered by filamentous green algae (Table 2). In 1984, all major communities of filamentous algae exhibited marked reductions in shoreline coverage. By 1985 some communities had already recovered their preneutralization abundance, although differences in taxonomy were apparent (Table 2).

In the two years prior to neutralization, the amount of shoreline affected by the waterline epilithic community remained relatively constant at 55–58%. Growth occurred as a narrow green band, 10 cm wide, firmly attached to shoreline rocks. Accumulations averaged <1 cm in thickness. This

TABLE 2. Shoreline development of filamentous algae in Bowland Lake observed during annual August or September surveys before (1982–83) and after (1984–85) neutralization. We describe algae found on rocks and logs as epilithic, those found on macrophytes as epiphytic, and those found aggregated and unattached as metaphytic. Primary metaphytic algae appeared as a reddish-purple "cloud" whereas secondary metaphytic algae appeared as a green "mat". ND = no data.

Community	Year	Shoreline covered (%)	Weighted mean Depth[a] Upper (cm)	Lower (cm)	Thickness (cm)	Dominant algae (%)
Waterline epilithic	1982	58	+10	0	<1	*Mougeotia* 99
	1983	55	+10	0	<1	*Mougeotia* 99
	1984	<1	+10	10	<1	*Bulbochaete* 49, *Mougeotia* 41
	1985	<1[d]	[f]	[f]	[f]	*Zygnema*[g] 59, *Mougeotia* 30
Submerged epilithic[c]	1982	ND	ND	ND	ND	ND
	1983	100[d]	0[d]	>150[d]	ND	ND
	1984	0[d]				
	1985	100[d]	0[d]	>200[d]	<1–1	*Oedogonium* 22, *Bulbochaete* 20, *Mougeotia* 19, *Zygnema*[g] 17
Epiphytic	1982	11	10	100	<2	*Mougeotia* 71
	1983	29	20	130	<1	*Mougeotia* 78
	1984	1	0	90	1	*Oeodogonium* 48, *Desmidium* 28, *Mougeotia* 19
	1985	15[d]	[f]	[f]	[f]	*Zygogonium*[g] 60
Primary metaphytic	1982	68	20	100	3	*Zygogonium*[g] 74
	1983	11	10	100	9	*Zygogonium*[g] 71
	1984	0				
	1985	<1[d]	[e]	[e]	[e]	*Zygogonium*[g] 100
Secondary metaphytic	1982	1	10	120	4	*Mougeotia* 43, *Spirogyra* 39
	1983	4	10	140	2	*Spirogyra* 44, *Mougeotia* 26, *Oedogonium* 23
	1984	2	0	80	3	*Mougeotia* 32, *Spirogyra* 31, *Desmidium* 16
	1985	<1[d]	[f]	[f]	[f]	*Microspora* 30, *Stigeoclonium* 21, *Tetraspora* 20, *Spirogyra* 18

[a]Values rounded to nearest 10 cm; genera representing greater than or equal to 15% of filamentous algal biovolume.
[b]Algae were above waterline at time of observation.
[c]This community is believed to have been widely distributed in 1982 consistent with conditions in 1983 and with our observations elsewhere in Ontario of year-to-year variability on algal occurrence (M.B. Jackson, unpubl. data; Turner et al. 1987).
[d]Estimated from qualitative lake survey.
[e]Estimated as similar to 1982–83 values from qualitative lake survey.
[f]Estimated as similar to 1982–84 values from qualitative lake survey.
[g]Later taxonomic analyses indicate that *Zygnema* and *Zygogonium* are likely the same species: *Zygogonium tunetanum*.

community was dominated by *Mougeotia* (99%) and was most evident on points of land exposed to increased wave action. In 1984 following neutralization, shoreline coverage was reduced to <1%, and *Bulbochaete* was the dominant alga. In 1985, minimal distribution was maintained, although *Zygnema* was now dominant. During postneutralization years, however, *Mougeotia* was still an important component of this waterline community.

In addition to the highly visible waterline band, virtually the entire littoral zone was covered by a very light filamentous "fuzz" which occurred quite uniformly on submerged rocks and logs from the waterline to maximum depths greater than 1.5–2.0 m. Although we made no record of the submerged epilithic community in 1982, it was noted in 1983, absent in 1984, and noted again in 1985 (Table 2). This submerged growth was assessed qualitatively: only its presence or absence, and approximate distribution, were recorded. Taxonomic samples were collected in 1985 only, at which time the community was primarily composed of a mixture of *Oedogonium* (22%), *Bulbochaete* (20%), *Mougeotia* (19%), and *Zygnema* (17%).

The epiphytic community showed marked differences between preneutralization years in the amount of shoreline affected (Table 2). Epiphytic cover varied from 11% in 1982 to 29% in 1983. Growth occurred as loosely attached green "fuzz" at 10–30 cm in depth, averaging <1–2 cm in thickness. Distributon was generally restricted to sheltered bays and, in 1983, to the lee of points of land in the main lake. The most abundant growth, however, always occurred near humic water inflows and seepage areas. *Mougeotia* (71–78%) dominated the epiphytic community during both control years. Following neutralization, shoreline coverage was only 1% in 1984, but increased again to preneutralization levels (15%) in 1985. The dominant postneutralization algae were *Oedogonium* in 1984, and *Zygogonium* in 1985. Based on further analyses, it appears that *Zygnema* and *Zygogonium* are likely the same species: *Zygogonium tunetanum* (M. B. Jackson, unpubl. data). However, verification of the species was not possible as reproductive structures were absent from the algal samples.

The metaphyton, or aggregated unattached algae, was characterized by two distinct communities. The more widespread and dominant community, referred to as the primary metaphyton, was characterized by reddish/purple clouds resting on or above a variety of littoral substrata. The primary metaphyton was dominated by *Zygogonium* (71–100%) (Table 2). Accumulations occurred at 10–100 cm in depth and averaged 3–9 cm in thickness. The thickest growths always occurred in relatively sheltered locations. The amount of shoreline affected

by this community varied considerably between preneutralization years: cover decreased from 68% in 1982 to only 11% in 1983. Following neutralization, growth was absent in 1984, and affected <1% of the lakeshore as *Zygogonium* in 1985.

The secondary metaphyton community typically occurred as a green "mat," usually on detritus, in close proximity to brown water inflows or seepage areas. In 1982 and 1983 the secondary metaphyton was composed largely of a mixture of *Mougeotia* (26–43%) and *Spirogyra* (39–44%), and to a lesser extent, *Oedogonium* (<15–23%) (Table 2). Growth occurred at 0–140 cm depth and averaged 2–4 cm in thickness. Although the length of shoreline affected by this community was never great, year-to-year differences were apparent. Cover increased from 1% in 1982 to 4% in 1983, due largely to distributional changes in the western inner bay. The shoreline occurrence of this community remained essentially unchanged in the years following neutralization, although *Microspora* (30%), *Stigeoclonium* (21%), and *Tetraspora* (20%) were dominant in 1985.

Macrophytes

A total of 15 macrophyte species was found in Bowland Lake in 1982 (Fig. 2), of which all were tracheophytes. Only three species could be regarded as frequent: *Eriocaulon septangulare*, *Lobelia dortmanna*, and *Myriophyllum tenellum*. These were found in most areas of the lake including exposed shores and sheltered bays. Another three species were commonly found only in sheltered bays: *Utricularia* sp., *Nymphaea odorata*, and *Scirpus subterminalis*. The nine remaining species were restricted to two large bays.

As macrophytes do not respond as quickly as filamentous green algae to changes in water chemistry, the macrophyte community was not resurveyed until the second postliming year (1985). A total of 15 macrophyte species were observed in Bowland Lake in 1985, of which 13 species occurred in 1982 (Fig. 2). There was little change from the 1982 preneutralization species composition or in the percent bottom coverage by macrophytes in the 60 sections surveyed. Percent bottom coverage was not significantly different for either areas with only recent inhabitation or areas with coverage in both pre- and postliming sampling years ($p>0.05$). The average percent bottom coverage was 31% in 1982 and 32% in 1985. The number of sections devoid of plants, however, decreased from 13 to eight. In sections where macrophytes were first noted in the second sampling year, the coverage was only 1% in three of the sections and 10% in the remaining two.

All but two of the macrophyte species recorded in 1982 were also recorded in the 1985 survey (Fig. 2). These two species, *Eleocharis acicularis* and *E. parvula*, were present in 1982 in only one of the sections. Two new taxa, *Nitella* sp. a charophyte, and *Brasenea schreberi*, were observed in 1985. *Nitella* sp. was found in minor amounts in only one section. *B. schreberi*, however, was found in two bays on the west side of Bowland Lake which were separated from each other by approximately 2 km of shoreline.

The macrophyte population had increased significantly in percent shoreline coverage in 1985 compared with 1982 ($p<0.05$) (Fig. 2). Most notable were the two *Myriophyllum* species, *M. farwellii* (4.0 to 11.0% shoreline coverage in 1982 and 1985, respectively) and *M. tenellum* (20.0 to 30.4%). The only species which decreased in abundance were *Utricularia* sp. (14.0 to 9.1%) and two species of *Eleochoris* which were not found in 1985. Although wild rice, *Zizania aquatica* was more widespread in 1985, the pure stands of 10–60% cover observed in 1982 were not observed in 1985. Instead, mixed stands of 5–10% cover of *Z. aquatica* with *M. farwelli* and /or *Eriocaulon septagulare* were found.

Discussion

Filamentous Algae

Neutralization by liming was effective at eliminating all previously extensive occurrences of filamentous green algae

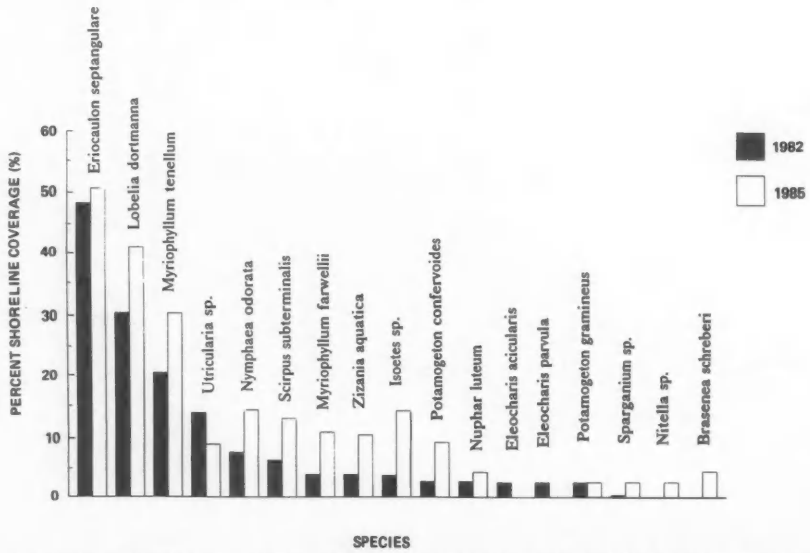

FIG. 2. Percent shoreline coverage of macrophyte species in 60 littoral zone sections of Bowland Lake in 1982 and 1985.

(hereafter referred to as fga) in Bowland Lake. There is already good evidence that fga increases in relative abundance as lakes acidify (Grahn et al. 1974; Hendrey and Vertucci 1980; Schindler 1980; Detenbeck and Johnson 1986; Turner et al. 1987). This paper, however, presents evidence supporting the reversal of fga occurrences by neutralization. These findings agree with Hultberg and Andersson (1982) who found that accumulations of *Mougeotia* almost vanished from an acidic Swedish lake during the first year after neutralization.

Within 2 yr after liming, Bowland Lake exhibited biological signs of early reacidification as indicated by increased epiphytic and submerged epilithic growths relative to the first postliming year. The first postneutralization pH depression below 6.0 occurred during the spring of the second postliming year (1985) (Table 1), although less acidic conditions predominated during most of the ice-free season. Hultberg and Andersson (1982) noted the return of increased algal growths within 5 yr of neutralization coincident with a pH depression below 5.5, and maximum pH values below 6.0. All of these findings are consistent with published acidification studies (Hendrey 1976; Muller 1980; Turner et al. 1987) that show that pH >6.0 is an important threshold relative to the predominance of certain fga in softwater lakes.

There are a number of mechanisms which could explain this relationship between lake acidity and fga abundance (Hendrey 1976; Stokes 1981, 1986). We can, however, dismiss the theory that differential rates of bacterial decomposition (Hendrey 1976) were responsible first for the elimination and then for the reoccurrence of fga growths in Bowland Lake. Viability of the fga was confirmed pre- and postneutralization by microscopic examination in the field. Accumulations of fga in acidic Lake L302 South were also composed of viable cells (Turner et al. 1987).

Changes in climate and nutrient levels were also dismissed as explanations of changes in fga growths. Meterologically the years were similar between 1982 to 1985. Air temperature and sunshine levels were similar between pre- and postliming years (t-test, $p>0.05$) as were lake water temperatures for both epilimnetic discrete depth and whole lake volume-weighted samples (t-test, $p>0.05$). While there were significant changes in epilimnetic nitrate and total phosphorus levels after neutralization ($p<0.05$), there were no significant differences ($p>0.05$) between the postliming years as the lake began to reacidify (Molot et al. 1990).

Of the remaining mechanisms, altered rates of grazing by macroinvertebrates may potentially be important (Hendrey 1976). Catches of the single species of crayfish (*Cambarus robustus*) more than doubled in the year following neutralization in Bowland Lake, while in the following year catches declined to preneutralization levels (W. Keller, unpubl. data). While there is evidence supporting herbivory of crayfish on macrophytes (Dean 1969; Lorman and Magnuson 1978), it is unlikely that a population change of this magnitude could result in such drastic changes in fga abundance. Evidence is lacking to support the hypothesis that diminished grazing pressure on fga, together with algal acid tolerance, results in increased fga biomass. Changes in macroinvertebrate grazing pressure have not accounted for the decline in algal abundance with reduced acidity in another study (Griffiths 1987).

It appears that either acid tolerance (Hendrey 1976) and/or dissolved inorganic carbon (DIC) limitation (Turner et al. 1987) are the primary factors responsible for the observed changes in the fga of Bowland Lake. Evidence suggests that both factors are potentially important. Specific pH preferences have been demonstrated for *Mougeotia* under controlled laboratory conditions (Turner 1985). Between pH 6.5 and 5.5 concentrations of bicarbonate decrease sharply, leaving CO_2, concentrations which are independent of pH, as the virtually sole species of DIC in the water column (Stumm and Morgan 1981). Perhaps the preference of certain fga for free CO_2 or their ability to utilize low concentrations of CO_2 explains their apparent increased growth rates under low DIC and low pH conditions (Moss 1973; Turner et al. 1987).

While all communities of fga in Bowland Lake, excluding the metaphyton at inflow mouths and seepages, were eliminated or greatly reduced with neutralization, their responses to reacidification were more variable. Consistent with the findings of Turner et al. (1987), both the epiphyton and submerged epilithon responded rapidly to early declines in pH. With continued reacidification we expect the epiphytic growths to become more abundant and possibly increasingly dominated by either *Mougeotia* or *Zygogonium*, to the exclusion of other epiphytic algae. The same applies to the waterline epilithon, which by 1985 had yet to show any increase in shoreline coverage. When lake pH stays below 6.0 continuously, metaphytic growths dominated by *Zygogonium* could also become increasingly widespread.

Compositional responses to reacidification for certain fga in Bowland Lake were different from our experience with an artificially acidified lake. *Zygogonium* dominated the epiphyton of Bowland Lake during reacidification, while *Spirogyra* was much more abundant in the epilithon of Lake 302 South at corresponding pH (Turner et al. 1987). This suggests that the relative impact of different growth-controlling factors may variably affect algal succession with changes in lake pH, and that development of algal biomass could be similarly affected. While acknowledging the potential impact of altered rates of grazing, we believe that evidence for direct chemical effects of lake neutralization and acidification on the abundance of certain fga has been strengthened by the Bowland Lake findings.

Macrophytes

The most conspicuous change in the macrophytes in Bowland Lake was the increased distribution of 70% of the taxa. There were no major differences in average percent bottom coverage or species composition between pre- and postneutralization periods. The increased distribution of macrophytes may, however, be a result of our increased boating activity on the lake as part of the whole neutralization project. Two very minor species, *Eleocharis parvula* and *E. acicularis*, disappeared and two new species, *Nitella* sp., and *Brasenea schreberi*, appeared in the second survey year. *Eleocharis acicularis* and *Brasenia schreberi* were frequent species in softwater lakes in central Ontario over a pH range of 4.7–7.0 (Yan et al. 1985). However, Catling et al. (1986) and Jackson and Charles (1988) found *B. schreberi* was not present in lakes with pH <5.0.

The small postneutralization changes in Bowland Lake were consistent with the work of Yan et al. (1985) who found in a survey of Ontario lakes which were not metal-contaminated that: (1) tracheophyte species richness was not correlated with pH in lakes with pH <5.2, and (2) *Eriocaulon septangulare* occurred in over 75% of the softwater lakes over a pH range of 4.6–7.0, while *Lobelia dortmanna* (42%) and *Myriophyllum tenellum* (35%) were widely distributed in the lakes. A survey of Adirondack lakes also demonstrated (1) and (2) above, although

the dominant macrophyte species differed (Roberts et al. 1985). The most common species in one Adirondack survey was *Utricularia purpurea* (Roberts et al. 1985), whereas Jackson and Charles (1988) found *Nuphar* spp. and *Eriocaulon septangulare* in 75% of their Adirondack lakes. *Utricularia* spp. were the fourth most common macrophytes in Bowland Lake.

In Scandinavian lakes macrophyte communities were relatively unaffected by neutralization except for the disappearance of *Sphagnum* mats (J. E. Fraser, General Research Corp., Virginia, pers. comm.). *Sphagnum* was rare in Bowland Lake prior to neutralization. Eriksson et al. (1983), in a survey of four limed lakes in Sweden, found that *Sphagnum* decreased considerably whereas helophytes increased in density. Some individual differences were noted such as the decrease in *Juncus bulbobus* in one lake (it remained unchanged in the two other lakes in which it was found) and the appearance of *Potamogeton natans* in two lakes; however, species richness, distribution area, and plant density remained largely unchanged.

Before this study began, it was suspected that because of the greater water clarity in some acidified lakes, Bowland Lake might support a deep-water macrophyte community (Singer et al. 1983). Our results suggest that this was not the case. On exposed shores, very few plants were seen in depths greater than 2 m. Only in one large, protected bay were plants abundant at a depth of 3 m. The deep-water transects revealed only one plant species in deeper water: a moss (i.e. Bryophyta), a patch of which was found at 12 m depth. Mosses typically colonize lakes at such depth (Light 1975; Spence 1967; Sheldon and Boylen 1977).

Spence (1982) surveyed data from 36 lakes and showed that the mean maximum depth limit of Tracheophytes was 4–6 m. Our finding that the depth of tracheophyte growth in Bowland Lake rarely exceeded 3 m seems unusual. The excellent water transparency in Bowland Lake would tend to favour greater depth of colonization. Potentially, substratum availability could restrict the depth distribution of macrophytes, but this seems unlikely. Observations from the deep water transect indicated suitable substrata of sand and gravel extending as deep as 6 m, with a mixture of sand and mud prevailing at deeper depths. For some lakes, it has been proposed that temperature limits the depth to which macrophytes grow (Spence 1964; Sheldon and Boylen 1977; Moeller 1980) especially in stratified lakes with high light penetration (Dale 1986); however, the temperature at 8 m in Bowland Lake was 11°C on June 3 and 19.2°C on August 18, 1982, indicating it would not appear to be a limiting factor.

Neutralization of Bowland Lake resulted in a decline of previously extensive growths of filamentous green algae, in particular Zygnematales. The short response time between the change in acidity and disappearance and reappearance of the fga suggests that the submerged epilithic and epiphytic communities may be important biological indicators or predictors of acidification or its reversal. The macrophyte community, composed mainly of tracheophytes, did not alter species richness in response to the decrease in acidity. However, increased percent shoreline coverage was noted for most species two years following liming. The significance of the increased macrophyte distribution and the mechanisms by which the fga and macrophytes respond to changes in acidity require further understanding.

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Changes in the Zoobenthos Community of Acidified Bowland Lake after Whole-Lake Neutralization and Lake Trout (*Salvelinus namaycush*) Reintroduction

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The zoobenthos of Bowland Lake is described prior to, and for 2 yr after, neutralization of the lake from pH 4.9 to >6.0 and reintroduction of lake trout (*Salvelinus namaycush*). Observed changes in the total abundance, biomass, and size structure of shallow and profundal zoobenthos assemblages were attributable to changes in the fish community, not to improvements in water quality. A shift toward increased importance of oligochaetes, more representative of nonacidic conditions, occurred. However, many common, acid-sensitive taxa of zoobenthos which were absent prior to neutralization had not appeared within 2 yr after treatment, indicating insufficient time for recolonization.

Les auteurs décrivent le zoobenthos du lac Bowland avant et au cours des 2 an suivant la neutralisation des eaux, dont le pH est passé de 4,9 à 6,0, ainsi qu'avant et aprés l'ensemencement du touladi (*Salvelinus namaycush*). Les variations observées de l'abondance totale, de la biomasse et de la répartition des tailles du zoobenthos des eaux peu profondes et profondes sont le résultat de variations de la faune piscicole et non d'améliorations de la qualité de l'eau. On a noté une plus grande abondance d'oligochètes, un indicateur de conditions non acides. Toutefois, de nombreux taxons ZOO benthiques communs sensibles à l'acidité n'étaient toujours pas présents 2 an après la neutralisation des eaux, ce qui révèle quela recolonisation n'avait pas encore eu lieu.

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Benthic invertebrate communities are damaged by the acidification of lakes. For example, certain mayflies (Schindler et al. 1985), snails (Okland and Okland 1980), crayfish (Malley 1980; France 1984), amphipods (Stephenson and Mackie 1986), and clams (Okland and Okland 1980) are rarely encountered in acidic lakes.

Reversing acidic conditions by the addition of neutralizing agents may allow acid-sensitive organisms to recolonize. However, reported responses of invertebrate communities to neutralization have been variable. Benthic invertebrate communities have shown both increases (Hultberg and Andersson 1982; Raddum et al. 1984), and decreases (Scheider et al. 1975; Hultberg and Andersson 1982) in abundance following lake neutralization, and differing responses have been observed between littoral and profundal benthic communities (Raddum et al. 1984).

In order to evaluate changes in the benthic invertebrate community and possible resulting effects on the fish community that accompanied neutralization (from pH 4.9 to >6.0), and reintroduction of lake trout (*Salvelinus namaycush*), studies of invertebrate communities in Bowland Lake were implemented under Ontario's Experimental Lake Neutralization Program. Bowland Lake (*Ao*, 109 ha; $\bar{z}$, 7.6 m; *z* max, 28 m) is an oligotrophic ($\bar{x}$ total phosphorus 5 $\mu g \cdot L^{-1}$) lake located 70 km north of Sudbury, Ontario.

The neutralization of Bowland Lake in August 1983, is outlined in Molot et al. (1986). Detailed changes in water chem-

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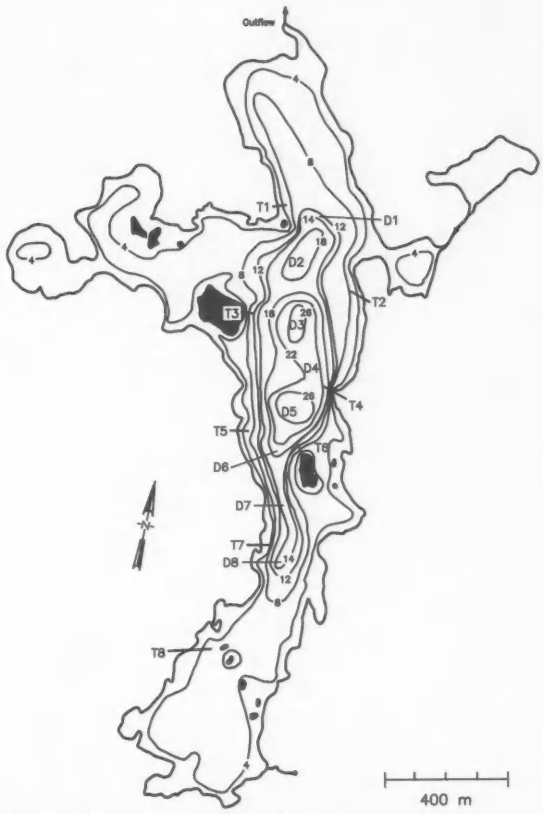

FIG. 1. Bathymetric map of Bowland Lake showing the profundal zone sampling sites (D1–D8) and shallow transects (T1–T8).

istry are given in Molot et al. (1990). Average postneutralization whole-lake pH was 6.5 in 1984 and 6.3 in 1985, in comparison to a preneutralization pH of 4.9 in 1983. Changes in the fish community, including lake trout introductions are described in Gunn et al. (1990). Briefly, lake trout stocking consisted of 1907 young-of-the-year, 502 yearlings, and 60 adults in 1983, and 200 3-yr-olds and 15 adults in 1985. Prior to lake trout introductions the fish community was dominated by abundant yellow perch (*Perca flavescens*).

Methods

Samples were collected from August 25–September 2, 1982, prior to neutralization, and from August 23–26, 1984 and August 27–September 2, 1985, after neutralization.

In 1982 and 1984, SCUBA divers took 10 5.2-cm diameter by 10-cm deep cores at approximately 1-m depth intervals along each of eight shallow (≤10 m deep) transects (T1–T8; Fig. 1). In 1984, an additional core was collected from each site along transects T1 and T7. Because analysis of 1982 and 1984 data showed no differences between transects, in 1985 the sampling effort was streamlined by collecting four replicate cores from each depth along transects T2 and T7 only. Cores of the same diameter were collected from eight profundal zone sites (D1–D8; Fig. 1) >10 m deep. One core was retained from each site in 1982, while four were taken from each site in 1984 and 1985.

All samples were preserved in the field with 10% formalin. In the laboratory, each sample was sieved through a 250-μm mesh screen. Invertebrates were hand-sorted into four size-classes: Class I, smallest; Class IV, largest (N. C. Collins, Department of Biology, University of Toronto, Erindale Campus, Mississauga, Ontario, pers. comm.) identified, enumerated, and stored in 75% ethanol. Different invertebrate taxa from the same size-class presented approximately equal profile areas to predators that visually locate prey. Average ash-free dry weights were determined for individual taxa within each size class.

Differences in abundance ($y = \mathrm{Ln}(x+1)$ transformed) and biomass ($y = \sqrt{(x)}$ transformed) between consecutive years were examined using a model III analysis of variance (ANOVA; Zar 1974). Differences within the four size-classes were examined using a model III multivariate analysis of variance (MANOVA, Barker and Barker 1984). If the MANOVA indicated that a significant difference existed, an ANOVA was conducted on the data from each size-class to determine where significant between year differences occurred.

Nonhierarchical classification analysis (Gauch 1982) was used to investigate changes in community composition between years. Chironomid and oligochaete assemblages were used as descriptors because these taxa dominated the zoobenthos biomass.

Results

Fifty-one, 58, and 66 zoobenthos taxa were identified in 1982, 1984, and 1985, respectively (Table 1). The increased number of taxa after neutralization was largely attributable to the appearance of additional species of benthic cladocerans and copepods in the collections (Table 1).

The total abundance (Fig. 2a) in the shallow (0–10 m) zone was lower in 1984, after neutralization, compared with 1982 ($p<0.01$) and remained so through 1985 ($p>0.05$). However, the total biomass (Fig. 2b) was not different in 1982 and 1984 ($p>0.05$), but was lower in 1985 compared with 1984 ($p<0.05$). This was attributable to an increase in mean organism size in 1984 followed by a decrease in 1985. Mean sizes were 44, 70, and 44 μg·animal^{-1} in 1982, 1984, and 1985, respectively. The abundance of size-class I was lower in 1984 compared with 1982 ($p<0.01$), but increased to preneutralization levels in 1985 ($p<0.01$, Fig. 2a). The abundances of size-classes II and III were higher in 1984 than in 1982 ($p<0.01$ and $p<0.05$, respectively). The abundance of size-class II decreased in 1985 ($p<0.01$), but remained the same for size-class III ($p>0.05$). There was no significant difference in size-class IV between years ($p>0.05$), although there was a slight, apparent decline in average abundance over the study period (Fig. 2a).

The total abundance (Fig. 2c) in profundal cores was lower in 1984 than in 1982 ($p<0.05$), but increased in 1985 compared with 1984 ($p<0.01$). The total biomass (Fig. 2d) was similar in 1982 and 1984 ($p>0.05$) but was lower in 1985 ($p<0.01$). Statistical analyses failed to detect significant differences in the abundance of the individual size classes between 1982 and 1984, although size-class I was more abundant in 1985 ($p<0.01$), while the abundance of size-class III was lower in 1985 compared with 1984 ($p<0.01$). The mean sizes of the profundal zoobenthos were 81, 118, and 48 μg·animal^{-1} in 1982, 1984, and 1985, respectively.

TABLE 1. Bowland Lake benthic invertebrate taxa list, 1982–85. Species indicated by an asterisk were represented by a single specimen.

Taxa	1982	1984	1985
Oligochaeta:			
Amphichaeta americana	P	P	P
Chaetogaster diaphanus	P	P	P
Nais communis	P	P	P
Pristina longiseta	P	P	P
Specaria josinae	P	P	P
Stylaria lacustris		P	P
Uncinais uncinata	P	P	P
Aulodrilus americana	P		P
Lumbriculus variegatus	P		
Naididae spp.	P	P	P
Arachnida:			
Arrenurus	P		
Hydrodoma despiciens	*	*	*
Lebertia		*	
Limnesia	P		
Forelia			P
Hydrochoreutes		*	
Piona	*		
Unionicola	P		
Amphipoda:			
Hyalella azteca	*		
Cladocera			
Eubosmina longispina			P
Acroperus harpae			P
Alona affinis		P	P
Alona costata		*	P
Alona guttata			P
Chydorus bicornutus			P
Eurycercus		P	P
Ceriodaphnia reticulata			P
Daphnia ambigua			P
Daphnia pulex		P	P
Holopedium gibberum	P		P
Leptodora kindtii		P	*
Acantholeberis curvirostris	P	P	P
Ilyocryptus spinifer			P
Ophryoxus gracilis	P	P	P
Latona setifera	P	P	P
Sida crystallina			P
Copepoda:			
Calanoida		P	P
Eucyclops speratus		P	P
Macrocyclops albidus	P	P	P
Mesocyclops leuckarti		P	
Paracyclops poppei		P	P
Ostracoda:			
Candona			P
Darwinae stevensoni		*	
Coleoptera:			
Hydroporus	*		
Dineutus	*		
Diptera:			
Ceratopogonidae	P	P	P
Chaoborus punctipennis	P	P	P
Chironomus salinarius type	P		P
Cryptochironomus	*	P	
Cryptotendipes		*	*
Dicrotendipes	P	P	P
Microtendipes	P	P	P
Nilothauma	P	P	P
Pagastiella			P
Paracladopelma galaptera	P	P	P
Phaenopsectra	P		
Polypedilum		P	P
Sergentia	P	P	P
Stempellinella			P
Tanytarsus	P	P	P
Protanypus	P	P	P
Epoicocladius		P	
Heterotanytarsus nudalis	P	P	P
Heterotrissocladius	P	P	P
Psectrocladius sp. A.	P	P	P
Psectrocladius sp. B	P	P	P
Synorthocladius		P	
Ablabesmyia mallochi	P	P	P
Procladius	P	P	P
Ephemeroptera:			
Leptophlebiidae		P	
Hemiptera:			
Rheumatobates rileyi		*	
Megaloptera:			
Sialis	P	P	P
Odonata:			
Cordulia shurtleffi	*		
Epicordulia princeps	P	P	P
Somatochlora cingulata			P
Trichoptera:			
Cheumatopsyche		*	
Oxyethira	*		P
Lepidostoma		*	
Ceraclea	*		P
Oecetis		*	P
Molanna	P	P	P
Agrypnia	P	P	P
Phylocentropus		P	P
Polycentropus	P	P	P
Pelecypoda:			
Sphaerium	P	P	P
Nematoda:	P	P	P
Planariidae:	P		*
Total number of taxa:	51	58	66

Eight taxonomic clusters were produced by the classification analysis of chironomids and oligochaetes (Table 2). The taxonomic composition of shallow communities differed among the three sampling years, although the chironomids *Tanytarsus* and *Procladius* were numerically abundant throughout the study. After neutralization, oligochaetes appeared in all shallow clusters while *Phaenopsectra* disappeared. The chironomids *Tanytarsus* and *Sergentia* numerically dominated the profundal community throughout the study. Additional taxa in the profundal taxonomic clusters that showed shifts in importance between years included *Protanypus, Ablabesmyia, Chaetogaster, Chironomus, Epoicocladius*, and *Nais communis* (Table 2). The abundance of *Chaoborus punctipennis* increased 10-fold in profundal cores from 142 to 568 to 1534 animals·m^{-2} in 1982, 1984, and 1985, respectively.

Discussion

Overall, changes in zoobenthos biomass and abundance in Bowland Lake were not extreme, with maximum between-year variations of about 25 and 35%, respectively, on a whole lake basis (Fig. 2). Zoobenthos biomasses for shallow samples from Bowland Lake (610–770 mg·m^{-2}) were within the wide range (approximately 100–1000 mg·m^{-2}) reported by Collins et al. (1981) for 14 central Ontario lakes ranging in pH from 4.6–8.1. Profundal zoobenthos biomasses (860–1300 mg·m^{-2}) were higher than average values reported by Dermott et al. (1986) for groups of central Ontario lakes ranging in pH from 4.6–7.7 (99–808 mg·m^{-2}); however, a larger and thus presumably less efficient, screen size (500 μm) was used for that study. No correlation between pH and zoobenthos biomass was observed by either Collins et al. (1981) or Dermott et al. (1986).

The slightly reduced zoobenthos abundance in the year following neutralization (1984) in comparison to preneutralization (1982) abundance may indicate a short-term negative influence by water quality changes or metal precipitation induced by neutralization (Molot et al. 1990). Previous studies have documented reduced zoobenthos abundance after lake neutralization (Scheider et al. 1975; Raddum et al. 1984). The corresponding increase in mean organism size in 1984 may reflect more favorable conditions for individual growth resulting from the overall decrease in abundance.

However, an alternate and more likely explanation is selective predation on smaller individuals by the very large 1983

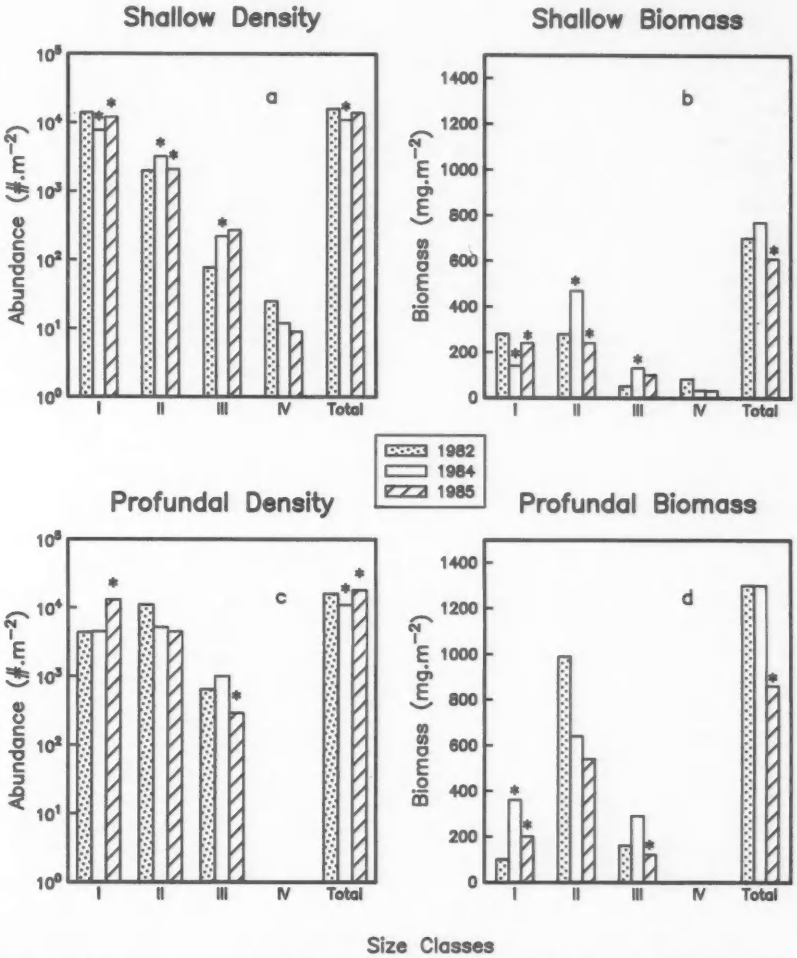

FIG. 2. Density and biomass of zoobenthos in the shallow and profundal zones of Bowland Lake in 1982, 1984, and 1985. Numbers indicate individual size-classes (I, smallest; IV, largest). An asterisk denotes a significant ($p<0.05$) difference from the previous year based on a MANOVA or ANOVA (see Methods). Note: log scale of abundance (a and c).

year class of yellow perch (*Perca flavescens*) (Gunn et al. 1990). Among invertebrate size classes, only size-class I in the shallow samples showed a significant decrease in abundance between 1982 and 1984. This supports the predation explanation, since small yellow perch may show a preference for shallower, nearshore areas (Sandheinrich and Hubert 1984).

Decreased biomass and reduced mean size of zoobenthos in 1985 likely resulted from increased predation by the very large cohort of 2+ (the same 1983 year class) yellow perch, and the introduced lake trout. Supporting evidence from fish studies (Gunn et al. 1990) indicates that decreased benthic food resources were manifested as declines in the growth and condition of both lake trout and perch. Post and Cucin (1984) documented substantial decreases in benthic invertebrate biomass and mean weight after introduction of perch to a small Precambrian Shield lake.

While small prey, including microcrustaceans, form a major portion of the diet of young-of-the-year yellow perch, macroinvertebrates become increasingly important in the diet of older perch (Nakashima and Leggett 1975; Keast 1977). Thus, the observed decreases in benthic biomass and mean size in 1985 are consistent with both increased overall perch and lake trout abundance and a shift in the prey size preference of the dominant perch age class. It is noteworthy that within size classes, significant decreases in abundance did occur in 1985 in both the shallow (size-class II) and profundal (size-class III) samples indicating increased utilization of deep water benthos by perch and/or lake trout.

The dominance of the zoobenthos community of Bowland Lake by Chironomidae is typical of oligotrophic, Precambrian Shield lakes (Cullis 1986; Dermott et al. 1986). The appearance of oligochaetes in all shallow clusters postneutralization (Table 2) suggests an effect by neutralization. Wiederholm and Eriksson (1977) and Crisman et al. (1980) indicated that worms are poorly represented in acidic lakes, and Dermott et al. (1986) observed Naididae only at pH >5.6. Scheider et al. (1975)

TABLE 2. Composition of clusters determined from the nonhierarchical classification analysis of chironomids and oligochaetes from Bowland Lake. Taxa are listed in order of their numerical abundance in the cluster.

Cluster	Composition	Zone	Year
1	*Tanytarsus, Phaenopsectra Procladius, Dicrotendipes*	Shallow	1982
2	*Procladius, Tanytarsus Dicrotendipes,* Naididae sp. A	Shallow	1984
3	*Tanytarsus, Procladius Amphichaeta,* Naididae sp. B	Shallow	1985
4	*Tanytarsus, Procladius* Naididae sp. B, *Amphichaeta*	Shallow	1985
5	*Tanytarsus, Sergentia Protanypus, Ablabesmyia*	Profundal	1982, 1984
6	*Sergentia, Tanytarsus Chaetogaster, Chironomus*	Profundal	1982, 1985
7	*Sergentia, Tanytarsus Epoicocladius, Nais communis*	Profundal	1984
8	*Tanytarsus,* Naididae sp. A *Heterotrissocladius, Procladius*	Shallow	1984

documented a four-fold increase in oligochaete abundance in Lohi Lake following elevation of lake pH from 4.4 to 7.0. The disappearance of *Phaenopsectra* from the shallow zone (Table 1) after neutralization agrees with the observations of Raddum et al. (1984) indicating reduced abundance of this taxon in a neutralized lake in Norway.

Acid-sensitive organisms such as gastropods (Okland and Okland 1980; Collins et al. 1981; Servos et al. 1985) were not collected in Bowland Lake postneutralization. Gastropods may be slow to colonize neutralized lakes (Eriksson et al. 1983) and may yet appear. Similarly, the colonization rates of other taxa, including amphipods and mayflies are apparently slow. *Hyalella azteca*, an acid-sensitive, very ubiquitous amphipod (Stephenson and Mackie 1986) was not observed postneutralization, although one specimen was found in 1982. Mayflies were only observed in 1984, and the taxon collected, *Leptophlebia*, is acid tolerant (Raddum et al. 1984).

The ten-fold increase in the abundance of *C. punctipennis* in profundal cores after neutralization is of significance, since *Chaoborus* is an important invertebrate predator and fish food item (Eriksson et al. 1980; Yan et al. 1982). Obviously, predation on *Chaoborus* by lake trout and perch was not a limiting factor in Bowland Lake, since *Chaoborus* increases corresponded with increased fish abundance (Gunn et al. 1990).

Overall, changes in the zoobenthos community attributable to neutralization were primarily taxonomic in nature, reflecting a shift to some taxa, particularly oligochaetes, more representative of nonacidic conditions. However, the continuing absence of many acid-sensitive taxa 2 yr after neutralization indicates that recovery of community composition typical of nonacidic lakes may be very slow. Predatory interactions with fish were apparently most important in determining zoobenthos abundance, biomass, and size structure. Thus, judicious (to avoid chemical extremes) neutralization of acidic lakes with residual fish populations should not lead to dramatic short-term changes in overall invertebrate abundance and biomass, unless fish abundance is directly affected.

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Survival, Growth, and Reproduction of Lake Trout (*Salvelinus namaycush*) and Yellow Perch (*Perca flavescens*) after Neutralization of an Acidic Lake Near Sudbury, Ontario

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Bowland Lake, an acidified lake (pH 4.8–5.2), was treated with calcite ($CaCO_3$) in 1983. Neutralization allowed for successful reproduction by reintroduced lake trout (*Salvelinus namaycush*). Mortality of lake trout embryos and juveniles in field toxicity tests decreased from 52–99% preneutralization to 0–30% postneutralization. The resident yellow perch (*Perca flavescens*) appeared unaffected by the chemical treatment. Both inter- and intraspecific competition were evident in the growth and body condition of perch and stocked lake trout in the years after neutralization. Springtime acid episodes continued to occur in the nearshore areas after the lake was neutralized, but no adverse effects on fish species were detected.

Le lac Bowland, un lac acidifié (pH de 4,8–5,2) a fait l'objet d'un apport de calcite ($CaCO_3$) en 1983. La neutralisation résultante des eaux a permis une excellente reproduction du touladi (*Salvelinus namaycush*) ensemencé. Le taux de mortalité des embryons et des juvéniles, déterminé au cours d'essais de toxicité sur le terrain, est passé de 52–99 %, avant la neutralisation, à 0–30 %, après la neutralisation. La population de perchaude (*Perca flavescens*) résidente n'a pas semblé être touchée par le traitement chimique. Au cours des années suivant la neutralisation, on a noté une compétition intra-spécifique et inter-spécifique portant sur la croissance et le facteur de condition de la perchaude et du touladi ensemencé. Après la neutralisation des eaux du lac, on a observé des périodes d'acidité printanière des eaux près du rivage mais aucune incidence négative sur les poissons.

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Liming is a recognized method to restore or maintain fish populations in acidic waters (Bengtsson et al. 1980; Eriksson et al. 1983; Nyberg 1984; Eriksson and Tengelin 1987). Liming generally improves water quality and increases survival of stocked or indigenous fish (Andersson et al. 1984; Schofield et al. 1986; Gloss et al. 1989), and occasionally creates conditions suitable for successful reproduction of reintroduced fish populations (Eriksson et al. 1983; Matzow et al. 1985).

Neutralization of lake water does not alter the acidic nature of incoming runoff water, and treated lakes can reacidify in relation to their flushing rate (DePinto et al. 1989). Short-term localized acidic conditions, such as the infusion of acidic snowmelt water, may also occur in neutralized lakes before more general whole-lake reacidification occurs (Hultberg and

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Andersson 1982; Wright and Skogheim 1983; Hasselrot et al. 1987; Molot et al. 1989). Therefore, fish species that are sensitive to episodic pH depressions in nearshore areas may not be protected by whole-lake neutralization. Lake trout (*Salvelinus namaycush*) appears to be a species that is particularly vulnerable to damage from acid episodes, because spawning usually occurs in shallow nearshore sites (McMurtry 1986) and early life stages are present in these areas during periods of snowmelt and runoff (Gunn 1989). However, there are few detailed studies of the factors affecting the recovery of fish populations in neutralized lakes, and none on lake trout.

In this study, we examined the effects of neutralization on survival, reproduction, and growth of introduced lake trout and resident yellow perch (*Perca flavescens*) in a lake near Sudbury, Ontario. Toxicity tests with early life stages of lake trout were conducted at nearshore sites to determine if whole-lake neutralization protected embryos from acid runoff events. Our overall objective was to test whether a self-sustaining lake trout population could be reestablished in a neutralized lake that continues to receive acidic runoff water.

Study Lakes

The treatment lake, Bowland Lake (47°05′N, 80°50′W), is located 70 km north of the Sudbury metal smelters. Prior to neutralization, Bowland Lake (*Ao*, 109 ha; $\bar{z}$, 7.6 m, *z* max., 28 m) was acidic (pH 4.8–5.2), dilute (conductivity 28–30 $\mu S \cdot cm^{-1}$) and clear (1.2–2.9 mg^{-1} dissolved organic carbon (DOC); 6–8 Secchi depth). Concentrations of smelter metals such as Cu and Ni were low (<5 $\mu g \cdot L^{-1}$). However, metals that are leached from watershed soils by acidic deposition, such as Al (100–180 $\mu g \cdot L^{-1}$) and Mn (79 $\mu g \cdot L^{-1}$) were elevated in Bowland Lake water. The lake was limed in August 1983 using 84 t of dry powdered limestone (96% $CaCO_3$, mean particle diameter = 9.3 μm). After the calcite addition, pH increased from 5.0 to 6.7, alkalinity increased from -0.3 to 4.5 $mg \cdot L^{-1}$, and Al concentration gradually declined from 130 to 30 $\mu g \cdot L^{-1}$. For further details on the chemical changes in Bowland Lake, see Molot et al. (1989).

Before neutralization the fish community of Bowland lake was severely affected by acidification. Native lake trout were extinct and the lake was dominated by a large population of yellow perch, a species relatively tolerant of low pH. A pre-neutralization attempt to reintroduce lake trout (stocked fall 1981: 8 $fish \cdot ha^{-1}$, age 2+) was unsuccessful (Gunn et al. 1987). Two other species, pearl dace (*Semotilus margarita*) and white sucker (*Catostomus commersoni*) have been observed in Bowland Lake, but because of their rare occurrence (only one specimen of each captured), these species are not considered in this paper.

Fowke Lake (*Ao*, 243 ha; $\bar{z}$, 14.4 m; *z* max. 53 m), a lake with a healthy reproducing lake trout population, was chosen as a reference lake for the bioassay experiments conducted on Bowland Lake. Fowke Lake (46°49′N, 79°40′W) is circumneutral (pH 6.9–7.3), dilute (conductivity 50–55 $\mu S \cdot cm^{-1}$), and contains low levels of Al (30–40 $\mu g \cdot L^{-1}$). The lake has a complex fish community, including abundant lake trout, lake herring (*Coregonus artedii*), yellow perch, white sucker, and cyprinids.

Materials and Methods

This paper reports results of a 6-yr study; 1 yr pretreatment and 5 yr posttreatment. Field toxicity tests were used to test whether toxic water quality existed before neutralization of Bowland Lake, and whether liming improved chemical conditions for trout. Lake trout were reintroduced to the treated lake in October 1983, 3 mo after neutralization. Survival, growth, and reproduction of lake trout were assessed annually during 1984–88. Population changes in the resident yellow perch, a potential prey of lake trout, were assessed each year.

Toxicity Tests

Lake trout eggs and juveniles were obtained from Lake Manitou (45°60′N, 82°00′W). Eggs were dry fertilized, then hardened and transported in water previously collected from Bowland Lake and Fowke Lake. Twenty incubators (each containing 50 eggs) were placed in mesh bags on the substrate at each of five nearshore sites (within 5 m of shore and in 1–2 m depth) on the two study lakes. The sites on Fowke Lake were known lake trout spawning sites (Ontario Ministry of Natural Resources, unpubl. data). The sites on Bowland Lake were selected to be similar to those on Fowke Lake and to spawning sites on other lakes with reproducing lake trout populations.

Mortality counts were conducted and water samples collected on three occasions, at mid-winter (January), late winter (March), and as soon as the lakes had become ice-free (May). Dead embryos were cleared in Davidson's solution and their developmental stage at time of death determined, according to Balon (1980). Fertilization success was determined on the first inspection of the eggs. Annual mortality rates of embryos were corrected for differences in fertilization rate, which varied from 82–99% between years. Water samples were analyzed for pH, conductivity, dissolved oxygen, temperature, Ca^{++} (only after 1983) and inorganic monomeric Al (OMOE 1981; LaZerte 1984).

Juveniles were used in toxicity tests conducted in the spring, with tests beginning a few days after the lakes became ice-free. At one to two sites per lake, young-of-the-year (0+) and yearling (1+) lake trout were held in five to six cages (20 fish per cage) suspended 0.25 m below the surface within 15 m of shore and in water depths of three to five metres. Mortality, pH, conductivity, dissolved oxygen, temperature, and inorganic Al were monitored daily during the test, which lasted 1–3 wk.

Additional toxicity tests were performed in early spring (April) using 0+ juveniles (1984–86). These tests were conducted beneath the ice during the season of heavy runoff, a potential worst case condition for juveniles. Cages (containing 20 fish) were anchored so that the top of the cage was just below the bottom of the ice. Water depths averaged approximately 1.5 m at three test sites, all within 6 m from shore on each lake. Survival was monitored daily for days 1–7, then on day 14 and day 21. Water samples were collected at 1, 14, and 21 d.

Lake Trout Stocking

Following neutralization, Bowland Lake was planted with lake trout of several different stocks. The initial planting in October 1983, consisted of 1907 young-of-the-year ($\bar{x}$ fork length (FL) = 89 mm) and 502 yearlings ($\bar{x}$ FL 216 mm) from North Bay hatchery (46°19′N, 79°28′W). In May of 1985, 200 3-yr-old trout ($\bar{x}$ FL 349 mm) from Hills Lake hatchery (47°30′N, 79°40′W) were planted into Bowland Lake.

Seventy-five adult lake trout were also introduced into Bowland Lake to quickly establish a reproducing trout population in the neutralized lake. Sixty adults (FL range = 540–920 mm) were transferred to Bowland Lake from Bark Lake (45°26′N,

77°51′W) ($N = 32$ fish) and Lake Manitou ($N = 28$ fish) in October 1983. An additional 15 adults (FL range = 324–581 mm) from Larder Lake (48°05′N, 79°53′W) ($N = 6$ fish) and Trout Lake (45°35′N, 80°10′W) ($N = 9$ fish) were planted in 1985.

Lake Trout and Yellow Perch Survey

A netting survey was conducted in September and October 1982, to assess the preneutralization status of yellow perch population. In 1983, and subsequent years, abundance, age, and size of fish species were assessed each spring and fall. Small (1.2 m pot; 1.2 cm stretched mesh) and large (1.8 m pot; 3.5 cm stretched mesh) trapnets were the principal fish collection gear, supplemented by small mesh (1.3 cm stretched monofilament mesh) gillnet, plexiglass traps (Trippel and Crossman 1981) and wire-mesh minnow traps. Angling was also used to collect lake trout for growth and diet studies.

Visual inspections of the shallow nearshore areas and shorelines were conducted immediately postneutralization to assess acute mortality of resident fish from the calcite addition.

Fork length and wet weight were measured and age determined for random samples of perch, ($n = 196$–893) and for all captured lake trout. Fulton's Condition Factor ($CF = wt/FL^3 \times 100$) was calculated for each fish. Age was estimated from scales. Some of the different age groups of lake trout were also distinguishable by unique fin clips applied prior to introduction. Stomach contents were collected from live lake trout ($n = 62$) in October 1988 using a stomach pump. Additional diet samples were obtained from gillnet collected fish captured in August 1984 ($n = 25$) and July 1988 ($n = 14$).

Lake Trout Reproduction

Spawning lake trout were located at sites along shorelines using underwater lights at night. Identified spawning sites were confirmed by SCUBA divers, who searched for eggs among the rubble. The surface area of each spawning site and the area of the watershed draining to this site were then estimated. Fry traps (Collins 1975) and shallow water emergence traps (J. G. Hamilton, unpubl. design), were placed above the substrate in the springtime to capture emerging alevins. Interstitial water samples were collected daily from within the substrate at four of the natural spawning sites during the spring melt period of 1986 (April 11–19) using the methods described in Gunn and Keller 1984).

Results

Lake Trout Toxicity Tests

The neutralization of Bowland Lake (Table 1) substantially increased survival of lake trout embryos (Fig. 1). Total survival during the over-winter toxicity test increased from 5% preneutralization to about 70% postneutralization. The greatest change occurred among the free embryos (posthatch), with survival increasing from 15% preneutralization to 86% in the year after neutralization.

Survival of age 0+ and 1+ juvenile lake trout increased from 1–48% in the preneutralization period to over 90% postneutralization (Fig. 2). Survival was high in both the spring under-ice and post-ice-melt toxicity tests. The increased survival of caged fish was consistent with observed increases in pH and declines in concentration of Al after neutralization (Table 1). Dissolved oxygen remained close to saturation during all years of the study. Water temperatures during the toxicity tests varied between test periods and from year to year (0.2–15°C), but remained within acceptable limits for lake trout.

Stocked Lake Trout Juveniles

The juvenile lake trout that were stocked in 1983 grew well (ca 8.0 $cm \cdot yr^{-1}$) for the first 2 yr postneutralization (Fig. 3). Approximately a year after the third group of lake trout was added to the lake (1985), growth ceased in all groups of trout, then resumed in the latter years of the study (Fig. 3). Body condition exhibited a similar pattern (Fig. 4). Declines in body condition were most severe in 1983 year class of North Bay fish (Fig. 4), the smallest and youngest stocked fish in the lake.

Stomach contents of lake trout collected in 1984 indicated that *Daphnia* were a common food item of age 1+ trout, while age 2+ fish fed more extensively on alderflies (*Sialis*), mayflies (*Leptophelbiidae*), and caddisfly pupae (*Polycentropodidae*). A few yellow perch were recorded in the stomachs of trout sampled in 1984. Yellow perch comprised 47.2 and 49.0% of

TABLE 1. Chemical conditions in the nearshore waters at bioassay sites on Bowland and Fowke Lakes. Data collected during egg (January–May) and yearling toxicity tests. Bowland Lake was limod in August 1983.

Bowland Lake	1983	1984	1985	1986	1987
pH	4.2–5.1	6.0–7.0	5.1–6.8	5.1–7.0	5.9–6.5
Conductivity ($\mu S \cdot cm^{-1}$)	30–35	35–49	31–51	19–40	35–45
Dissolved oxygen ($mg \cdot L^{-1}$)	10–12.9	9.6–13.8	10.4–13.4	9.8–13.0	7.1–11
Temperature (°C)	1.0–9.9	0.2–11.0	0.5–15.0	0.5–14.0	0.5–9.0
Ca ($mg \cdot L^{-1}$)	—	—	3.4–5.5	1.7–4.7	3.0–4.4
Total Al ($\mu g \cdot L^{-1}$)	100–160	52–150	19–160	20–310	25–97
Inorganic Al ($\mu g \cdot L^{-1}$)	—	—	1–6	3–251	0–17
Fowke Lake					
pH	5.7–7.6	6.0–7.3	5.9–7.3	6.1–7.5	6.8–7.4
Conductivity ($\mu S \cdot cm^{-1}$)	48–54	42–71	40–58	35–86	37–60
Dissolved oxygen ($mg \cdot L^{-1}$)	10.8–13.2	9.8–13.6	8.6–13.4	9.4–13.0	10–12
Temperature (°C)	1.0–10.3	0.5–11.0	0.2–11.9	1.0–15.0	1.0–9.5
Ca ($mg \cdot L^{-1}$)	—	—	6.1–8.3	1.9–8.3	3.4–8.5
Total Al ($\mu g \cdot L^{-1}$)	12–100	15–150	13–176	5–340	16–170
Inorganic Al ($\mu g \cdot L^{-1}$)	—	—	1–12	1–49	0–9

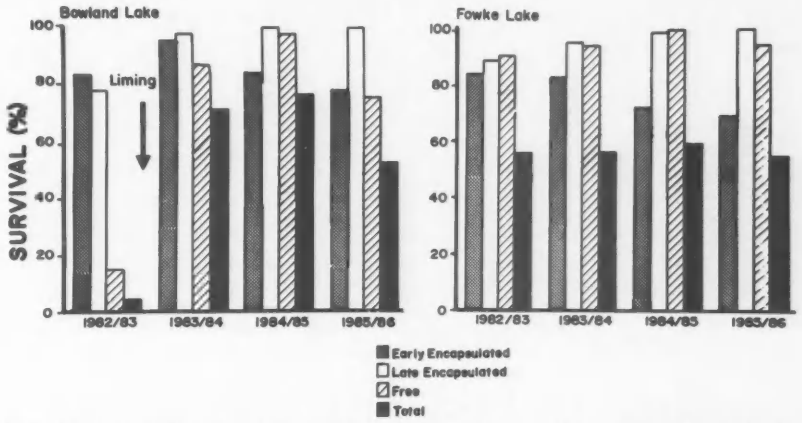

FIG. 1. Survival of lake trout embryos in Bowland Lake and a control lake, Fowke Lake, during the winters of 1982/83–1986/87. Percent survival indicated for early encapsulated (fertilization — occurrence of pigmentation of eyes), late encapsulated (pigmented eyes — hatch), and free (hatched embryos with attached yolk sac) embryo developmental periods.

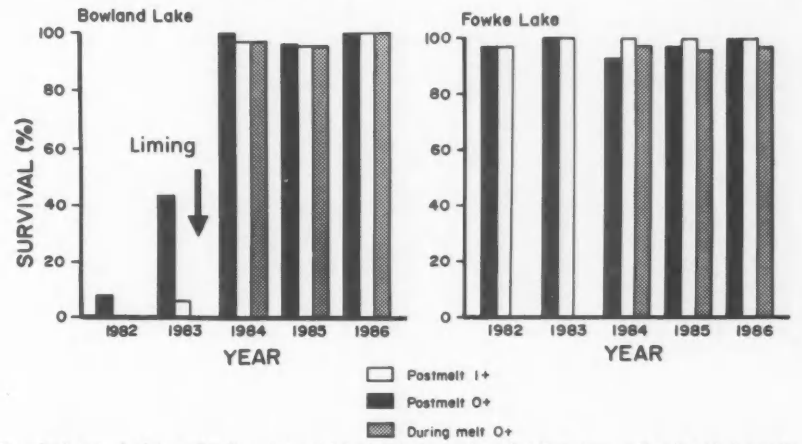

FIG. 2. Survival of juvenile (0+, 1+ yr) lake trout at nearshore holding sites on Bowland Lake and a reference lake, Fowke Lake, 1982–86. Survival during the under-ice tests in April and open-water tests in May are indicated.

the diet of lake trout sampled in the summer and fall of 1988, respectively (Table 2). The average length of perch consumed by lake trout was 5.1 cm in the summer and 7.1 cm in the fall. Predation on yellow perch was not restricted to larger lake trout. Perch were also found in the stomachs of three young (age 3+ and 4+) lake trout. Plankton cladocerans were numerically abundant but comprised little of the total weight of the stomach contents. Benthic invertebrates (mainly Tricoptera, Hemiptera, Coleoptera, and Diptera) comprised a significant part of lake trout diet sampled in summer (52.7%) but only 4.4% of the diet sampled in the fall (Table 2). Crayfish and miscellaneous items, including small mammals, were also present in lake trout sampled in the fall.

Stocked Adult Lake Trout

Introduced adult lake trout spawned in the limed lake. A single spawning site was discovered in the southern portion of the lake in 1984. In 1985 spawning activity was widespread at five sites along the shoreline of the lake basin and islands. Two of these sites were used again in 1986. No spawning was observed in 1987, but was observed again in 1988. Spawning sites were small (1–8 m^2) and very shallow (0.1–1.5 m) (Table 3). Most of the sites were located along island shores or other areas with small watersheds (only one exception, site 5), and hence would not likely receive large inputs of terrestrial runoff (Table 3). The substrate at the selected spawning sites was a shallow layer of granitic rubble (5–25 cm diameter) overlaying bedrock.

Depressed pH (min. 5.4) and elevated concentrations of potentially toxic Al (max. 167 $\mu g \cdot L^{-1}$ inorganic Al) were detected in the interstitial water of only one of the natural spawning sites during the spring sampling period of 1986 (Table 3). At the other sites the minimum observed pH and maximum concentration of inorganic Al were 6.2 and 43 $\mu g \cdot L^{-1}$, respectively.

The spawning activity of the introduced adults produced recruits. Emergence traps collected five alevins (23.5 ± 0.6 mm

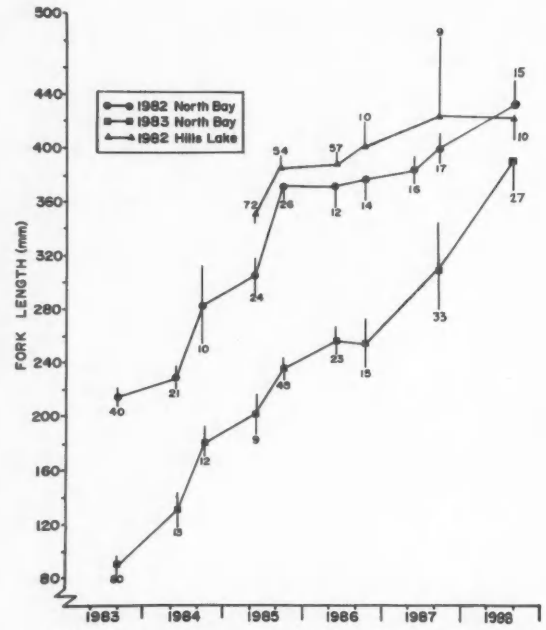

FIG. 3. Growth of three groups of stocked lake trout in Bowland Lake after neutralization. Sample means ± 1 SE and *N* are indicated. Some of the limits are not shown to improve clarity.

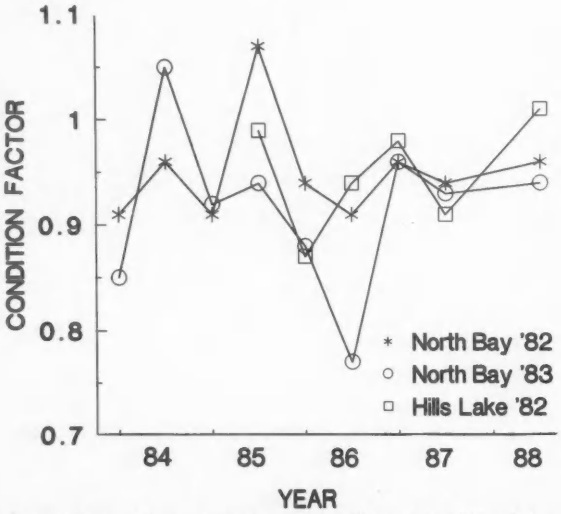

FIG. 4. Seasonal changes in body condition (Fulton's Condition Factor — $wt/LT^3 \times 100$) of stocked lake trout in Bowland Lake during 1984–88. Sample size at collection date are the same as in Fig. 3.

total length) in 1986. Six naturally produced juveniles were captured in fine mesh gillnets in 1988. The oldest of these were age 4+, indicating that introduced adults spawned successfully immediately after introduction in the fall of 1983.

Yellow Perch Population

No immediate mortality of yellow perch was observed following liming of Bowland Lake. A strong 1983 year-class of perch, produced 2 mo prior to neutralization, dominated trapnet catches in each of 1984 (74.8%), 1985 (36.7%), and 1986 (45.14%) (Fig. 5). Strong year-classes of perch again appeared in 1986 and 1988.

TABLE 2. Summary of stomach contents of lake trout in Bowland Lake in 1988. Values are presented as percent of total wet weight of stomach contents. Sample sizes (*n*) are the number of stomachs containing food.

	Percent of total	
Food item	Summer ($n=14$)	Fall ($n=40$)
Yellow perch	47.2	49.0
Plankton	0.1	0.3
Benthos	52.7	4.4
Crayfish	0	30.2
Miscellaneous	0	16.1

The relative abundance of perch (measured as fall trapnet catches) declined by five-fold immediately after neutralization and the reintroduction of lake trout in 1983. The catch of yellow perch reached a low of five fish per net set in the fall of 1987 (Fig. 6).

There was an initial increase in the growth rate of older (age 3+–4+) yellow perch following neutralization and stocking of lake trout (Fig. 7). The increase may be in part due to cannibalism of older fish on the young-of-the-year from the strong 1983 year class. However, growth and body condition of all ages of perch generally declined during the posttreatment period (Fig. 7, 8). The decline in growth continued in spite of low perch abundance in 1986–87. Resumption of growth and increases in body condition occurred in 1988.

Discussion

Calcite additions to Bowland Lake increased the lake water pH above the level reported to be associated with recruitment failure (pH <5.5–5.6; Beggs and Gunn 1986; Mills et al. 1987) and extinction (pH <5.2, Beggs et al. 1985) of lake trout and allowed for the reestablishment of reproduction and at least some recruitment to the juvenile stage within 5 yr of the chemical treatment.

Acid episodes (min. pH 4.3; max. total Al 800 $\mu g \cdot L^{-1}$) continued to occur in surface waters (top 1 m) of Bowland Lake after neutralization (Molot et al. 1989). However, the low levels of mortality in the nearshore bioassays (postneutralization) and the capture of natural recruits in Bowland Lake diminishes the concern about the potential impact of acidic runoff water on early life stages of lake trout. The spawning sites in Bowland Lake were in very shallow water (<20 cm), but were in areas where runoff was minimal due to small subwatersheds or proximity to steep shoreline (Table 2). As a consequence, spawning sites on Bowland Lake did not appear particularly vulnerable to damage from acidic runoff water.

Mills (1984) showed that acidic episodes during snowmelt were not required for reproductive failure of lake trout in acidifying lakes. In his study, lake trout suffered recruitment failure when the average whole lake pH (without episodes) was artificially lowered to 5.6 (total Al 40 $\mu g \cdot L^{-1}$). No significant mortality of early life stages of lake trout occurred during the winter or spring, but mortality occurred between the time of emergence of alevins from the substrate in May (postsnowmelt) and the fall of the first year of life. Gunn (1989) reported similar results for Whitepine Lake (pH 5.6–5.8), a lake where acidic

TABLE 3. Physical characteristics of spawning sites selected by adult lake trout after neutralization of Bowland Lake. Selected chemical characteristics of interstitial water sampled during April 9–19, 1986 are also indicated.

Site	Substrate size (cm)	Area of egg deposition (m^2)	Water depth (m)	Extent of watershed	pH	Ca^{++} ($mg \cdot L^{-1}$)	Inorganic Al ($mg \cdot L^{-1}$)
1	5–25	8	0.3–1.5	nil[a]	6.5–6.9	3.1–4.0	11–19
2	5–10	2	0.1–1.0	nil[a]	5.4–6.6	3.0–3.4	31–167
3	1–15	10	0.2–1.0	small[b]	6.4–6.7	3.1–4.0	0–28
4	10–15	4	0.2–1.0	small[b]	6.2–6.6	2.1–3.4	15–43
5	5–15	1	0.1–0.3	large[c]	NA	NA	NA

[a]On ledge at base of vertical rock face.
[b]On shoreline of small island.
[c]Large forested area of about 25 ha.

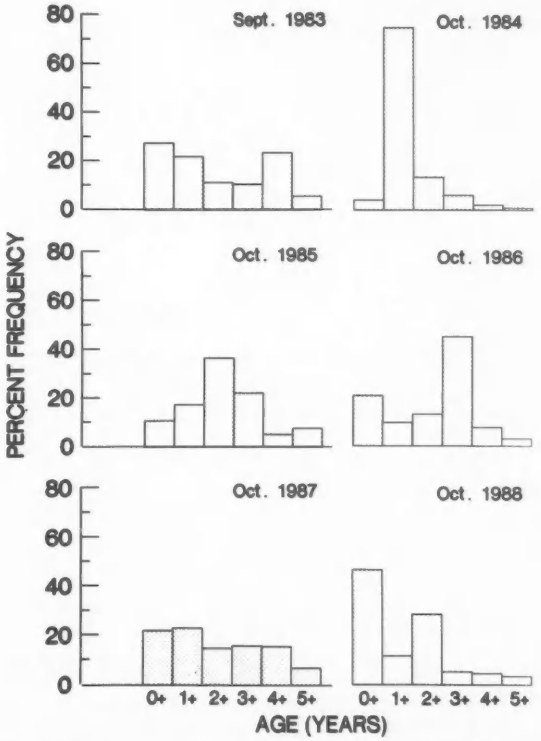

FIG. 5. Age class composition of yellow perch in Bowland Lake, 1983–88. Fish were collected using small mesh (1.2 cm) trapnets during the fall of each year.

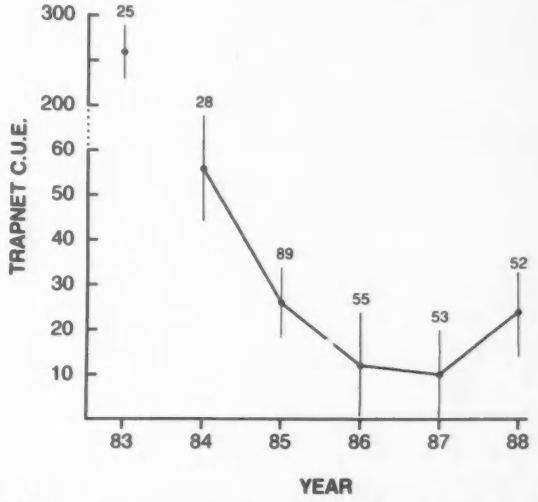

FIG. 6. Trapnet catch-per-unit effort (CUE; number per 24 h) of yellow perch in Bowland Lake, 1983–88. Collections in 1983 were conducted in September. Netting occurred in October in the other years. Mean CUE ±1 SE and number of samples are indicated.

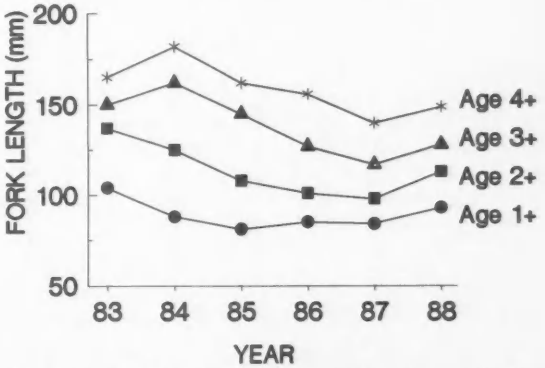

FIG. 7. Length at age of yellow perch in Bowland Lake, 1983–88.

runoff events occurred (minimum pH 4.5), but were too brief (1–5 d) and shallow (<1 m deep) to cause substantial mortality of embryos within the spawning substrate.

Our finding that episodic acidification was not critical to lake trout survival in Bowland Lake must be approached cautiously before extrapolating to other systems. Lakes with flushing rates greater than Bowland Lake can have deep penetration of runoff water (Schofield et al. 1986). Therefore, episodic acidification may have major deleterious effects on recruitment success in some lakes, including neutralized lakes. Episodic acidification also remains a serious problem in some streams and rivers (Henrikson et al. 1984).

Although Nyberg et al. (1985) noted increases in perch (*P. fluviatilis*) populations in neutralized lakes in Sweden, increases in year-class strength of yellow perch in Bowland Lake are likely related to water temperatures rather than neutralization.

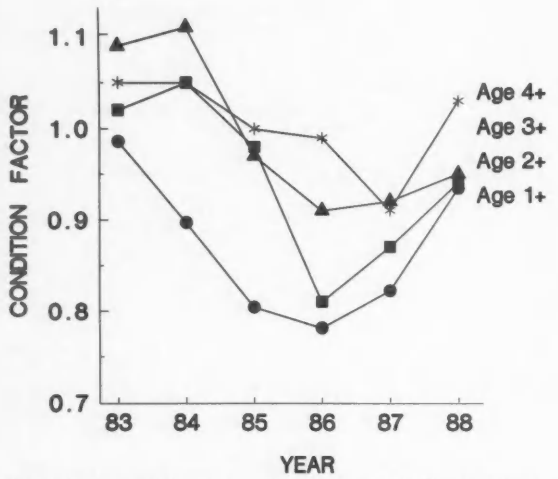

FIG. 8. Body condition at age of yellow perch in Bowland Lake, 1983–88.

The largest year class of perch in Bowland Lake was spawned in the spring of 1983, prior to neutralization. Mean monthly air temperatures recorded at Sudbury airport (Environment Canada, unpubl. data) 52 km southeast of Bowland Lake in June, July, and August were significantly warmer (ANOVA; $p \leq 0.05$) in 1983 than in other years of the study. Water temperatures were assumed to follow the same relationship as air temperature (McCombie 1959). Year-class strength for natural populations of yellow perch can vary widely (up to 40×) (Forney 1971; Clady 1976; Koonce et al. 1977), and has been found to be positively correlated to water temperature (Clady 1976).

The simultaneous occurrence of a strong 1983 year-class of perch with the stocking of hatchery reared lake trout appears to have increased competition for food. Keller et al. (1989) reported that biomass and mean size of littoral zone zoobenthos, a prey of both lake trout and perch, declined in 1985 in Bowland Lake from preneutralization (and fish stocking) levels. Similarly, Post and Cucin (1984) documented substantial decreases in benthic invertebrate biomass and mean weight after introduction of perch to a small Precambrian Shield lake.

Growth ceased and body condition of lake trout declined following the introduction of the third group of trout in 1985, despite a relatively low density of introduced lake trout (ca 3.0 kg/ha) in Bowland Lake. The simultaneous decline in both growth and condition of lake trout and the older yellow perch provided further evidence that food availability limited growth. In the most recent year of the study, growth rate and body condition of the lake trout returned to levels typical of similar age fish in other stocked populations (Powell et al. 1986; Gunn et al. 1987). Feeding on the abundant 1986 and 1988 year classes of yellow perch, and/or reduced intraspecific competition through natural mortality appear to be the explanation(s) for the observed recovery in growth and body condition in lake trout.

It is significant to note that yellow perch comprised almost one-half of the total diet of lake trout sampled in the summer and fall. This indicates that the trout are able to feed on yellow perch throughout the summer period despite thermal stratification of the lake. Therefore, predation by introduced lake trout is the likely explanation for the substantial decrease in abundance of the yellow perch following neutralization.

The Bowland Lake experiment demonstrated that liming can produce short-term improvements in water quality of an acidified lake and allow for successful reproduction of a salmonid population, even when acid episodes continue to occur at nearshore sites. However, the long-term effectiveness of such treatments and the recolonization rates of other components of the indigenous biotic community are uncertain.

Acknowledgements

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OBITUARY / NÉCROLOGIE

Dr. John Reginald Dingle
1921–1989

The scientific community was saddened in May 1989, to learn of the passing of Dr. "Jack" Dingle at his home in Halifax. He had been retired since 1979 from the Halifax Fisheries Technological Laboratory after a distinguished 30-yr career devoted to researching the complex physical and chemical changes occurring in fresh and frozen fish.

Dr. Dingle attended Dalhousie University where he obtained both a Bachelor's (1940) and a Master's (1942) degree in chemistry. He was an outstanding student and received the Governor General's Gold Medal in 1941. During World War II he maintained his devotion to scientific research by serving at the Canadian Naval Research Establishment in Halifax. Following the war he attended both Harvard University and the University of Toronto and earned a Ph.D. in chemistry. From 1949 until his retirement in 1979 he was a leading member of the research team at the Halifax Technological Laboratory that gained world recognition for its studies on the undesirable chemical changes that take place in fish muscle even after freezing. Dr. Dingle and his colleagues were world leaders in this field and their work stimulated a global surge of research on frozen fish muscle.

Dr. Dingle was primarily a protein physical chemist who delved into the mysteries of fish muscle chemistry at a time when the techniques for separating and isolating proteins were far more difficult and time-consuming than they are today. Nevertheless he made major advances regarding the protein composition of fish muscle and the undesirable changes induced by frozen storage. Other research investigations contributed to a better scientific understanding of why some fish species spoil more rapidly than others. He demonstrated that differences in the concentrations and biochemical activities of the tissue enzymes responsible for the breakdown of ATP (adenosine triphosphate) and TMAO (trimethylamine oxide) accounted for many of the spoilage variations in fresh and frozen fish. In addition, he found that the mincing of fish could accelerate deterioration and that minced fish formulations should avoid the inclusion of rapid-spoiling species and of enzyme-rich kidney tissue.

The majority of Dr. Dingle's many scientific papers can be found in the Journal of the Fisheries Research Board of Canada (now Can. J. Fish. Aquat. Sci.) and his results are still being quoted in the scientific literature today. He made a solid contribution in this field and was highly respected by his colleagues around the world. Fellow employees found him to be an excellent problem solver and as a caring individual he was always ready to share his expertise and knowledge with others. Even after retirement he continued to serve as a valuable external advisor to the graduate student research program in fisheries at the Technical University of Nova Scotia. He was an active member of several scientific organizations and served in an executive capacity with the Nova Scotian Institute of Science, the Chemical Institute of Canada, and the Atlantic Fisheries Technological Conference.

In addition to his many contributions in the field of seafood science, Dr. Dingle will be long remembered for his outstanding photographs of Atlantic seascapes which will continue to adorn many a wall in the Maritimes.

E. Graham Bligh
Technical University of Nova Scotia
Halifax, N.S. B3J 2X4

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTES PUBLICATIONS

VOLUME 46, No. 7 — article by R. M. Peterman: *Application of statistical power analysis to the Oregon coho salmon (Oncorhynchus kisutch) problem.*

Page 1185, Fig. 1: Legend should read "...Curves show the upper or lower values of k...".

VOLUME 46, No. 8 — article by A. T. Charles: *Bio-socio-economic fishery models: labor dynamics and multi-objective management.*

Page 1318, Equation (20): Regrettably two typesetters' errors occurred in this equation. In the numerator, $\ldots + T + (L/ax\pi)\ldots$ should read $\ldots + T \cdot (L/ax\pi)\ldots$; in the denominator, $\ldots \cdot B_L \cdot \beta\alpha\pi\ldots$ should read $\ldots \cdot B_L \cdot \{\alpha\pi\ldots$.

VOLUME 46, No. 9 — article by B. M. Jessop and W. E. Anderson: *Effects of heterogeneity in the spatial and temporal pattern of juvenile alewife (Alosa pseudoharengus) and blueback herring (A. aestivalis) density on estimation of an index of abundance.*

Page 1566, Topic sentences of the last paragraph of the left-hand column and the first paragraph of the right-hand column were partly transposed by the printer after proofs were checked. These paragraphs should read, respectively:

Among-species differences in temporal and coarse scale spatial density value and pattern were evaluated by five biweekly, synoptic surveys of the headpond, composed of 61 randomly selected cells divided among strata in....

and

Among- and within-species variability in medium scale spatial and nightly temporal density was examined by replicating 3 times a series of 32....

VOLUME 46, No. 10 — article by A. Mazumder, W. D. Taylor, D. J. McQueen, and D. R. S. Lean: *Effects of fertilization and planktivorous fish on epilimnetic phosphorus and phosphorus sedimentation in large enclosures.*

Page 1740, Table 1: In the bottom row (internal loading or net imbalance) the values for the $+N$ and $+NF$ treatments should read -1.04 and -1.25, respectively.

VOLUME 46, No. 11 — article by B. R. Ward, P. A. Slaney, A. R. Facchin, and R. W. Land: *Size-biased survival in steelhead trout (Oncorhynchus mykiss): back-calculated lengths from adults' scales compared to migrating smolts at the Keogh River, British Columbia.*

Page 1853, part of the sentence beginning on line eight of the abstract was inadvertently omitted from the original version, which reversed our intended meaning; it should read: "BSL increased with increased years spent in fresh water but decreased with increased years in salt water, based on ageing adults' scales."

VOLUME 46, No. 12 — article by J. W. Parks, A. Lutz, J. A. Sutton, and B. E. Townsend: *Water column methylmercury in the Wabigoon/English River–Lake system: factors controlling concentrations, speciation, and net production.*

Page 2184, B. E. Townsend (Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba R3T 2N6) was inadvertently deleted from the by-line list of authors. The bibliographic strip at the head of the abstract is the correct full reference for this article.

VOLUME 47, No. 1 — article by J. P. Sullivan, H-L. Lai, and V. F. Gallucci: *A catch-at-length analysis that incorporates a stochastic model of growth.*

Page 197, Equation: regrettably due to typesetters' error an equation was omitted from the top of the page. The equation reads as follows:

$$k_{\Delta_s} = k \left\{1 + \frac{C}{2\pi}\left[\sin\left(\frac{2\pi}{n}(1 + \Delta s)\right) - \sin\left(\frac{2\pi}{n}(\Delta s)\right)\right]\right\}$$

VOLUME 46, No. 11 — review by R. H. Parrish, R. Serra, and W. S. Grant: *The monotypic sardines, Sardina and Sardinops : their taxonomy, distribution, stock structure, and zoogeography.*
Pages 2023 and 2024, Figs. 2 and 3: regrettably the light shading on these distribution maps was lost upon reproduction. The correct illustrations are:

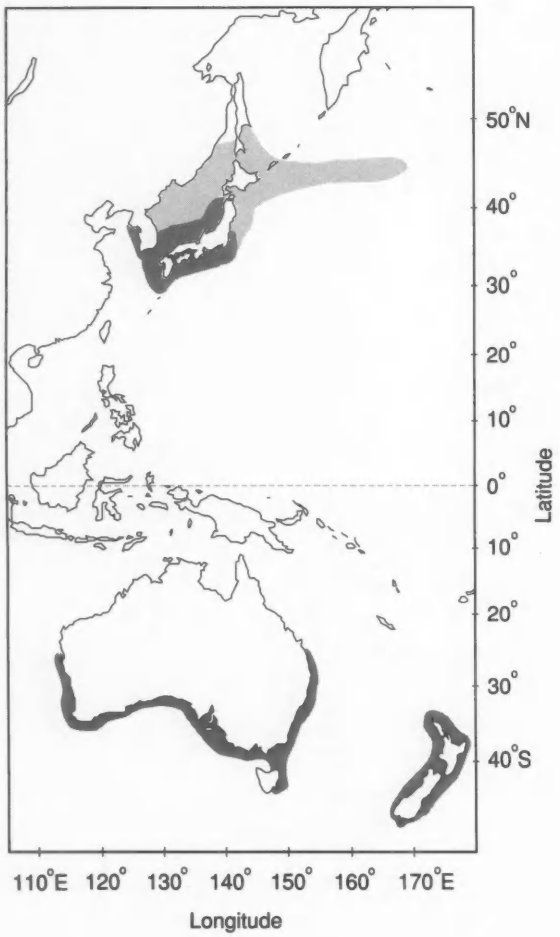

FIG. 2. Distribution of *Sardinops* in the eastern Pacific at low abundance (dark shading) and the increase in range that occurs at high abundance (light shading).

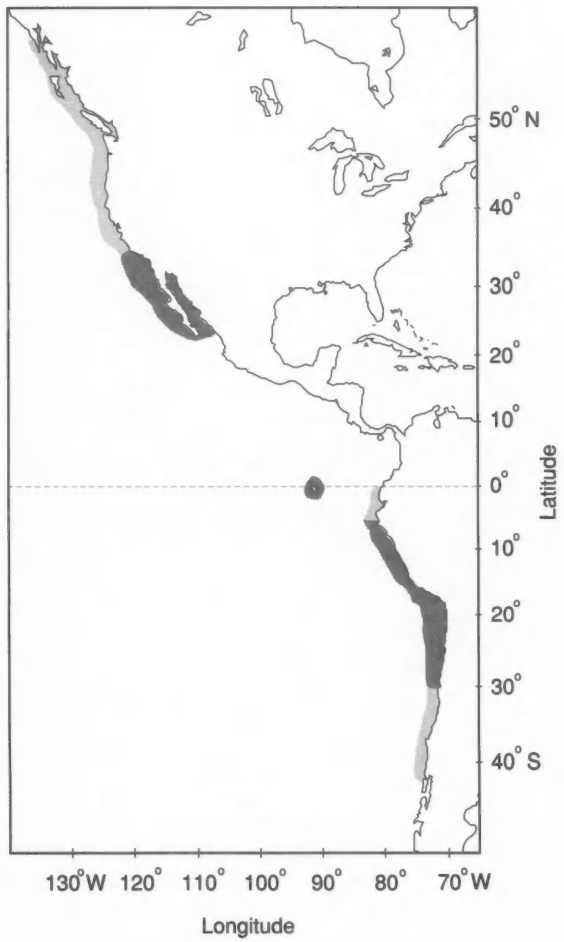

FIG. 3. Distribution of *Sardinops* in the Indo-Pacific at low abundance (dark shading) and the increase in range that occurs at high abundance (light shading).

ANNOUNCEMENT/AVIS

NATO Advanced Study Institute on Individual Cell and Particle Analysis: Multidisciplinary Applications to Oceanography

An Advanced Study Institute on individual cell and particle analysis, sponsored by NATO Scientific Affairs Division, will be held in Acquafredda di Maratea (near Naples), Italy, from October 21 (arrival) to October 30 (departure), 1990. The organising committee is as follows:

Dr. Serge Demers (Canada), Director
Dr. Clarice M. Yentsch (U.S.A.)
Dr. Peter H. Burkill (U.K.)
Dr. Marlon R. Lewis (Canada)
Dr. Daniel Vaulot (France)
Dr. Sallie W. Chisholm (U.S.A.)
Dr. Donato Marino (Italy)

Sixty oceanographers and ecologists working in fields related to individual particle analysis (i.e. marine optics, flow cytometry, image analysis, and remote sensing) will have the opportunity to explore the application of these methodologies to a wide range of oceanographical problems. The morning sessions will be dedicated to presentations by invited speakers (oceanographers, physiologists, biochemists, and physicists). Subjects include: bulk versus individual cell measurements, optics of particles, light scattering properties of cells, biophysics of light absorption and emission by photosynthetic pigments, flow cytometry and image analysis in oceanography, fluorescent probes, food web dynamics and remote sensing.

The Study Institute is primarily tutorial in scope, but there will be a certain amount of time allocated to short contributions that are relevant to the topics treated by the invited speakers.

Total attendance at the meeting is limited . For further details and an application form contact: Dr. Serge Demers (ASI Director), Maurice Lamontagne Institute, Fisheries and Oceans, P.O. Box 1000, Mont-Joli, Québec, Canada, G5H 3Z4. Telephone: (418) 775-6521. Telemail (Omnet): S. DEMERS. FAX: (418) 775-6542. Telex: 051-3815. Deadline for application submissions: 15 March 1990.

This workshop will also be supported by funds from the following sources: Maurice Lamontagne Institute (Fisheries and Oceans Canada); Centre du St-Laurent (Environment Canada); NASA; Centre National de la Recherche Scientifique (France).

Conférence d'études avancées de l'OTAN sur l'analyse individuelle des particules: Applications multidisciplinaires à l'océanographie.

Une conférence d'études avancées, parrainée par la Division des affaires scientifiques de l'OTAN, sera tenue à Acquafredda di Maratea (près de Naples), en Italie, du 21 octobre au 30 octobre 1990. Le comité organisateur regroupe les personnes suivantes:

Dr Serge Demers (Canada), Directeur
Dr Clarice M. Yentsch (É.-U.)
Dr Peter H. Burkill (U.K.)
Dr Marlon R. Lewis (Canada)
Dr Daniel Vaulot (France)
Dr Sallie W. Chisholm (É.-U.)
Dr Donato Marino (Italie)

Environ soixante océanographes et écologistes intéressés aux problèmes reliés aux particules auront l'opportunité d'explorer l'application de différentes méthodologies (flux cytométrie, analyseur d'image, télédétection) permettant de résoudre différents problèmes océanographiques. Les sessions du matin seront dédiées à des présentations données par des conférenciers invités (océanographes, physiologistes, biochimistes et physiciens). Les sujets traités toucheront différents aspects de l'analyse des particules: mesures globales versus mesures sur une base individuelle, optique des particules, propriétés diffusantes des cellules, biophysique et pigments, application de la flux cytométrie et des analyseurs d'images en océanographie, étude de la physiologie par utilisation de marqueurs fluorescents, chaîne alimentaire microbienne et télédétection.

Quoique ce type de conférences comporte principalement des travaux dirigés, une certaine période sera allouée à de courtes présentations connexes aux sujet traité par les conférenciers invités.

Le nombre de participants à la réunion est limité. Pour plus de détails et les formulaires d'application contacter: Dr Serge Demers (Directeur ASI), Institut Maurice-Lamontagne, Pêches et Océans, Boîte Postale 1000, Mont-Joli, Québec, Canada, G5H 3Z4. Téléphone: (418) 775-6521. Télémail (Omnet): S. DEMERS. FAX: (418) 775-6542. Télex: 051-3815. Date limite pour les applications: 15 mars 1990.

Cet atelier de travail est également supporté financièrement par les organismes suivants: Institut Maurice-Lamontagne (Pêches et Océans Canada); Centre du St-Laurent (Environnement Canada); NASA; Centre National de la Recherche Scientifique (France).

The Atlas of Alberta Lakes

edited by Pat Mitchell and Ellie Prepas

to be published by the University of Alberta Press in 1990

The Atlas of Alberta Lakes brings together all available information on 100 Alberta lakes on the basis of their recreational and economic importance and data available. The Atlas has been compiled over the past four years with assistance from the Alberta government, the Recreation, Parks, and Wildlife Foundation, and the University of Alberta, and has been received with enthusiasm everywhere sample chapters have been distributed.

The chapters on each lake are designed to provide all the information a lake user would need, without sacrificing their usefulness to the scientist or lake manager. The first part of each chapter is a summary of lake location, access, fisheries, land use, and facilities, in nontechnical terms. The remainder is detailed technical information on the drainage basin: soils and plant communities; lake basin, including inflows, outflows, and water levels; water quality, including detailed graphs and information on water temperature and dissolved oxygen, ion and nutrient chemistry; and biota including fish species, commercial, sport, and domestic harvests and species introduction and population changes; and wildlife in the immediate vicinity.

A fairly extensive introduction or ''users' guide'' to the book will explain the scientific terms and concepts used in each chapter. A full-page map showing the location of all 100 lakes will be included in the introduction and other figures will be in four colours. The Atlas will have an 11″ × 14″ format, with approximately 450 pages, containing 600 tables, 600 drafted figures, 100 photographs, bibliography, general reference list, and glossary.

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The Atlas of Alberta Lakes

édité par Pat Mitchell et Ellie Prepas

sera publié par les Presses de l'Université de l'Alberta en 1990

The Atlas of Alberta Lakes rassemble toute l'information disponible sur 100 lacs de l'Alberta choisis en fonction de leur valeur récréative et économique et des données existantes. L'information a été compilée ces quatre dernières années avec l'aide du gouvernement provincial, de la Recreation, Parks and Wildlife Foundation et de l'Université de l'Alberta. Les chapitres qui ont été distribués jusqu'à maintenant ont suscité des réactions très enthousiastes.

Les chapitres portent chacun sur un lac; ils contiennent tous les renseignements nécessaires aux gens qui fréquentent les lacs, mais aussi aux scientifiques et aux gestionnaires. La première partie de chaque chapitre présente un résumé où l'on décrit en termes simples l'emplacement du lac, la façon de s'y rendre, les espèces qui y sont pêchées, l'utilisation des terres et les installations qui se trouvent sur place. Suivent des renseignements techniques plus détaillés sur: le réseau hydrographique; les sols et les plantes; le bassin lacustre, y compris sur les affluents et les effluents et sur les niveaux d'eau; la qualité de l'eau, avec graphiques détaillés et données sur la température de l'eau, l'oxygène dissous, les ions et les nutrients présents; le biote, y compris sur les espèces de poisson, les prises des pêcheurs commerciaux, sportifs et autochtones, les espèces introduites et les changements observés au niveau des populations; et la faune des environs immédiats.

L'introduction ou ''guide de l'utilisateur'' explique les termes scientifiques et les concepts utilisés dans chaque chapitre. Une carte occupant une pleine page et montrant l'emplacement des cent lacs sera incluse à l'introduction; les autres figures seront en quatre couleurs. L'Atlas mesurera 11″ × 14″ et comptera environ 450 pages; on y trouvera 600 tableaux, 600 figures, 100 photographies, une bibliographie, une liste d'ouvrages de référence et un glossaire.

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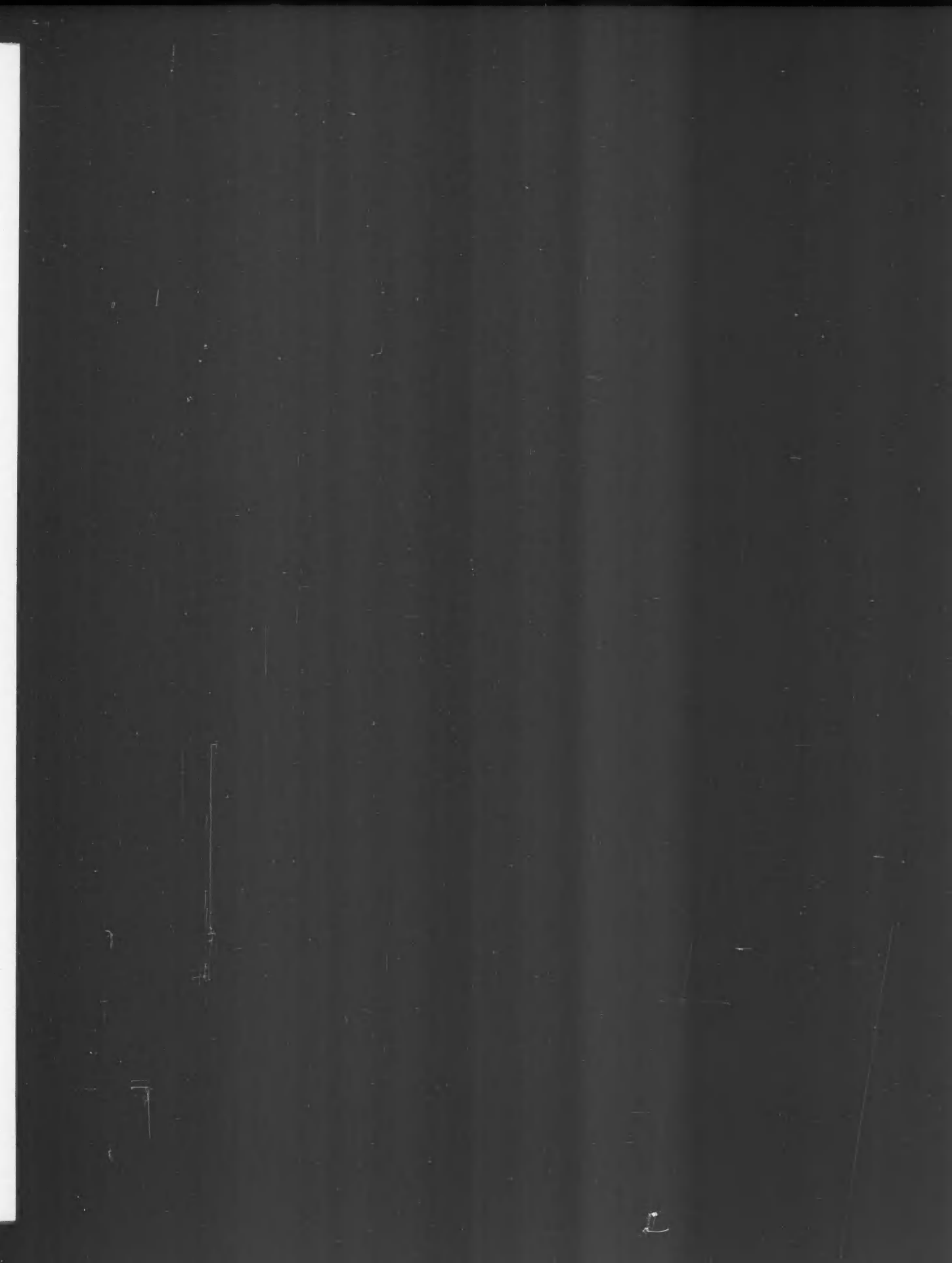
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